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Volume 19, Numbers 1 and 2 January 31, 1975

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A NEW CRAWFISH OF THE GENUS *PROCAMBARUS*, SUBGENUS *CAPILLICAMBARUS*, FROM TEXAS, WITH NOTES ON THE DISTRIBUTION OF THE SUBGENUS

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Abstract

A new species is described, on the basis of 43 first form males from Brazoria County, Texas. New distributional records for *Procambarus hinei* and *P. incilis*, the other known members of the subgenus, include ten new county records. The ranges suggest that rivers are significant barriers separating these species from one another.

Introduction

The species of *Procambarus* described here occurs in the lower Brazos River valley, between the ranges of *P. hinei* (Ortmann, 1905) and *P. incilis* Penn (1962), the other two known members of the subgenus *Capillicambarus* Hobbs (1972). Collected by the author in the spring of 1972, this crawfish also has been found in collections made in 1966 by Joe B. Black of McNeese State University, Lake Charles, Louisiana.

I wish to thank Dr. Black for very generously providing data on all his Texas collections of the subgenus *Capillicambarus*, and for loaning several of them to me. I am also most grateful to Horton H. Hobbs, Jr. of the Smithsonian Institution for his criticism of the manuscript, and to Chester O. Martin for his assistance in the preparation of the figures. This is contribution No. TA10099 of the Texas Agricultural Experiment Station.

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Procambarus (*Capillicambarus*)
brazoriensis new species

Diagnosis.—Body and eyes pigmented. Rostrum usually without marginal spines or tubercles in adults, acumen poorly or not at all delimited basally. Juveniles with acute lateral spines at base of acumen. Areola broad but variable, 2.5 to 4.9 times longer than wide, and 28.3 to 33.6% of entire length of carapace. Single cervical spine present or absent, often so small as to escape notice. Postorbital ridges weakly developed, terminating anteriorly in short spine or ending squarely, with no spine. Antennal scale 2.1 to 2.5 times longer than wide, broadest slightly proximal to midlength. Chela subcylindrical and non-tuberculate. Ischia of third and fourth pereiopods with simple hooks. Venter of cephalothorax covered with dense mat of long hairs arising from mesial faces of pereiopods and third maxillipeds. First pleopods (Fig. 1-A, B) symmetrical, extending forward just beyond caudal margin of coxae of third pereiopods when abdomen is flexed. Apical third of pleopod bent caudad at about 35° angle to shaft, expanding distally as seen in mesial view, not tapering toward apex, terminating abruptly in three small elements. Apical elements twisted (sinistrally on left appendage) as

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Table 1. Measurements (mm) of *Procambarus brazoriensis*.

	Holotype	Morphotype	Allotype
Carapace:			
Length	15.2	14.2	17.3
Greatest height	8.3	7.8	9.3
Greatest width	7.6	7.1	9.1
Areola:			
Length	5.1	4.4	5.7
Least width	1.2	1.2	1.4
Rostrum:			
Length	4.1	3.9	5.0
Width at base	2.5	2.4	3.1
Antennal scale:			
Length of lateral margin	4.2	4.0	4.2
Greatest width	1.9	1.7	2.0
Chela:			
Length of outer margin	13.6	9.6	7.3
Length of inner margin of palm	8.4	5.4	3.1
Greatest width of palm	3.0	2.3	2.7
Greatest thickness of palm	2.6	1.8	1.8
Length of dactyl	4.6	3.8	3.6

in other members of subgenus (Penn, 1953, 1962), but twisting slight so that elements best observed in mesial or lateral view. Mesial process non-corneous, spiculiform, extending laterodistad; cephalic process somewhat corneous, lying closely mesiocephalic to mesial process, strongly compressed laterally, tapering gently in mesial view from wide base to blunt or truncate tip; central projection corneous, acute, compressed along longitudinal axis, with fusion line of component elements visible. Caudal process absent. Apical half of pleopod with dense covering of long hairs on mesial surface; cephalomesial shoulder weak.

Holotypic male, Form I.—Cephalothorax (Fig. 1-C, D) subovate. Abdomen narrower and slightly longer than cephalothorax. Greatest width of cephalothorax subequal to height at same level. Areola 4.2 times longer than wide. Rostrum without lateral spines, widest at base, with margins converging as nearly straight lines; no median carina. Suborbital angle slightly greater than right angle. Branchiostegal spine small, acute. Cervical groove interrupted by small lateral spine on each side. Epistome (Fig. 1-H) broader than long, with small spine on anterior margin. Cephalic portion of telson with two spines at each caudolateral angle, more lateral one nearly twice length of other. Antennules of usual form, with basal segment bearing large spine on distal margin of ventral surface. Antennae reaching just beyond telson. Antennal scale (Fig. 1-I) extending well beyond tip of rostrum, broadest slightly proximal to midlength; lateral margin straight, terminating in acute spine.

Chela (Fig. 1-E) very finely pubescent. Palm inflated; both fingers terminating in corneous tips. Opposable margins of fingers flattened, covered with rows of minute rounded denticles, with about four rows distally to about ten proximally. Fingers short; length of dactyl 34% that of outer margin of chela. Carpus subcylindrical, nontuberculate.

Hooks on ischia of fourth pereiopods about one-third as long as those on third pereiopods (Fig. 1-J). Hook on latter extending proximally beyond distal margin of corresponding basis; that on fourth pereiopod not reaching proximal margin of ischium.

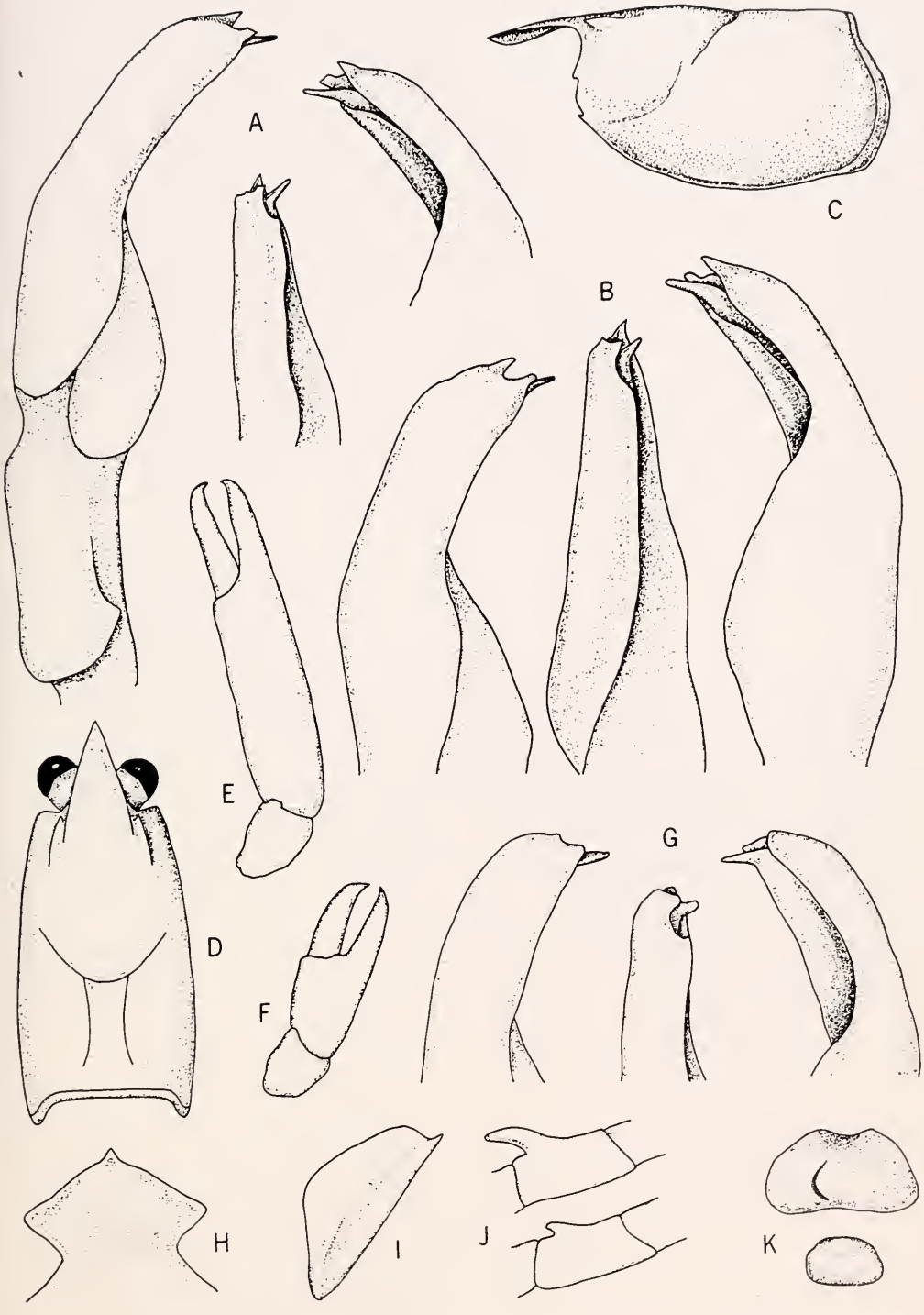
Hairs on venter of cephalothorax especially thick and conspicuous on mesial faces of third maxillipeds and first three pereiopods.

First pleopods as described in diagnosis. Measurements are given in Table 1.

Morphotypic male, Form II.—Similar to

→

Figure 1. *Procambarus* (*Capillicambarus*) *brazoriensis* new species. A, mesial, caudal, and lateral views (left to right) of first pleopod of paratypic male, Form I; B, similar views of first pleopod of another paratypic male, Form I; C, D, lateral and dorsal views of carapace of holotype; E, chela and carpus of holotype; F, chela and carpus of allotype; G, mesial, caudal, and lateral views of first pleopod of paratypic male, Form II; H, I, epistome and antennal scale of paratypic male, Form I; J, ischia of third and fourth pereiopods of holotype; K, annulus ventralis of paratypic female. Pubescence removed from all structures illustrated.


A
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holotype in general appearance. Chelae reduced but with ratio of finger length to total length of chela as in holotype. Hooks on ischia of third and fourth pereiopods greatly reduced; those on third pereiopods extending proximally barely to margin of ischium, and those on fourth pereiopods appearing only as low prominences. Venter of cephalothorax only sparsely clothed with long hairs. Apical processes of first pleopods (Fig. 1-G) reduced, non-corneous.

Allotypic female.—Similar to holotype in shape and structure of cephalothorax, but differing markedly in proportions of chela (Fig. 1-F), in which length of inner margin of palm and of dactyl subequal. Annulus ventralis (Fig. 1-K) freely movable; width nearly twice as great as length. Annulus in caudal view tapering steeply to truncate apex. Anterior face with deep furrow from base to summit. Sinus originating at summit, running posterodextrad and gently recurving posterosinistrad nearly to base of posterior face. Sternal plate immediately caudal to annulus with acute apex directed cephaloventrad.

Color pattern.—The following notes are based on live and freshly killed specimens. A pair of brown to dark olivaceous dorsal stripes, each slightly wider than the areola, originate behind the eyes and run posteriorly along either side of the areola and onto the abdomen. On the abdomen, these stripes converge slightly, become narrower, and terminate on the base of the telson. The mid-dorsal region, from rostrum to base of telson, is light tan, appearing as a light stripe narrower than the darker stripes bordering it. Another dark stripe, generally brown and narrower than the first, begins on the mid-lateral surface of the carapace and extends to the base of the uropod. The space between this stripe and the edge of the abdominal tergites is about as wide as the stripe. The latter areas, and the broader regions between dorsal and lateral dark stripes, are light tan to pale olive, as are the telson, uropods, and chelae.

Size.—The largest specimen collected is a female, 19.4 mm in carapace length. The largest and smallest Form I males have corresponding lengths of 18.0 and 12.0 mm.

Type locality.—Ditch beside County Road 400, 0.1 mile SE of Missouri Pacific railroad and 0.25 mile SW of Brazos River, at S edge of Brazoria, Brazoria County, Texas. Specimens were netted from the ditch, which lies between the gravel road and a grazed live oak woodland with lush undergrowth. A portion of the ditch over a hundred meters long and about one meter wide commonly contains water up to 0.3 m deep, but dries completely during extended periods without rain. *Procambarus acutus* (Girard, 1852), *P. clarki* (Girard, 1852), and *Cambarellus puer* Hobbs (1945) were collected at the same locality.

Types.—The holotypic male, Form I, allotypic female, and morphotypic male, Form II (Nos. 133916, 133917, 133918, respectively) are deposited together with 50 paratypes (15 ♂ I, 12 ♂ II, 10 ♀, 6 juv. ♂, 7 juv. ♀) in the National Museum of Natural History, Smithsonian Institution. The remaining paratypes (27 ♂ I, 33 ♂ II, 56 ♀, 81 juv. ♂, 88 juv. ♀) are in the collection of the author.

Range.—Procambarus brazoriensis has been found only in Brazoria County, Texas, in an area between the San Bernard River and Oyster Creek (both sides of the Brazos River), extending inland from the Gulf only about 20 miles (Fig. 2). It has been collected by the author or by J. B. Black at the following localities: S edge of Brazoria (DWA T14-1), 1 mi. NE Brazoria (JBB 144, 145; DWA 415), 4.3 mi. NE Brazoria (DWA 408), 5 mi. NE Brazoria (JBB 143), 2.5 mi. S Brazoria (DWA T14-5), and 1.5 mi. N Jones Creek (DWA T14-2).

Variation.—The range of variation in the first pleopods of the 43 Form I males examined is represented in Fig. 1-A, B. Non-secondary sexual characters vary as indicated in the diagnosis. In about 20% of females the annulus ventralis appears as a mirror image of that of the allotype.

Relationships.—Procambarus brazoriensis has its closest affinities with *P. hinei*. In comparison with *P. incilis*, both *P. hinei* and *P. brazoriensis* have a more slender mesial process, a much better developed cephalic process, and a more acute central projection. The hooks on the ischia of the fourth pereiopods of *P. brazoriensis* are similar to those of *P. hinei*, and are much better developed than those of *P. incilis*. These similarities and differences indicate that *P. brazoriensis* is not an intergrade between

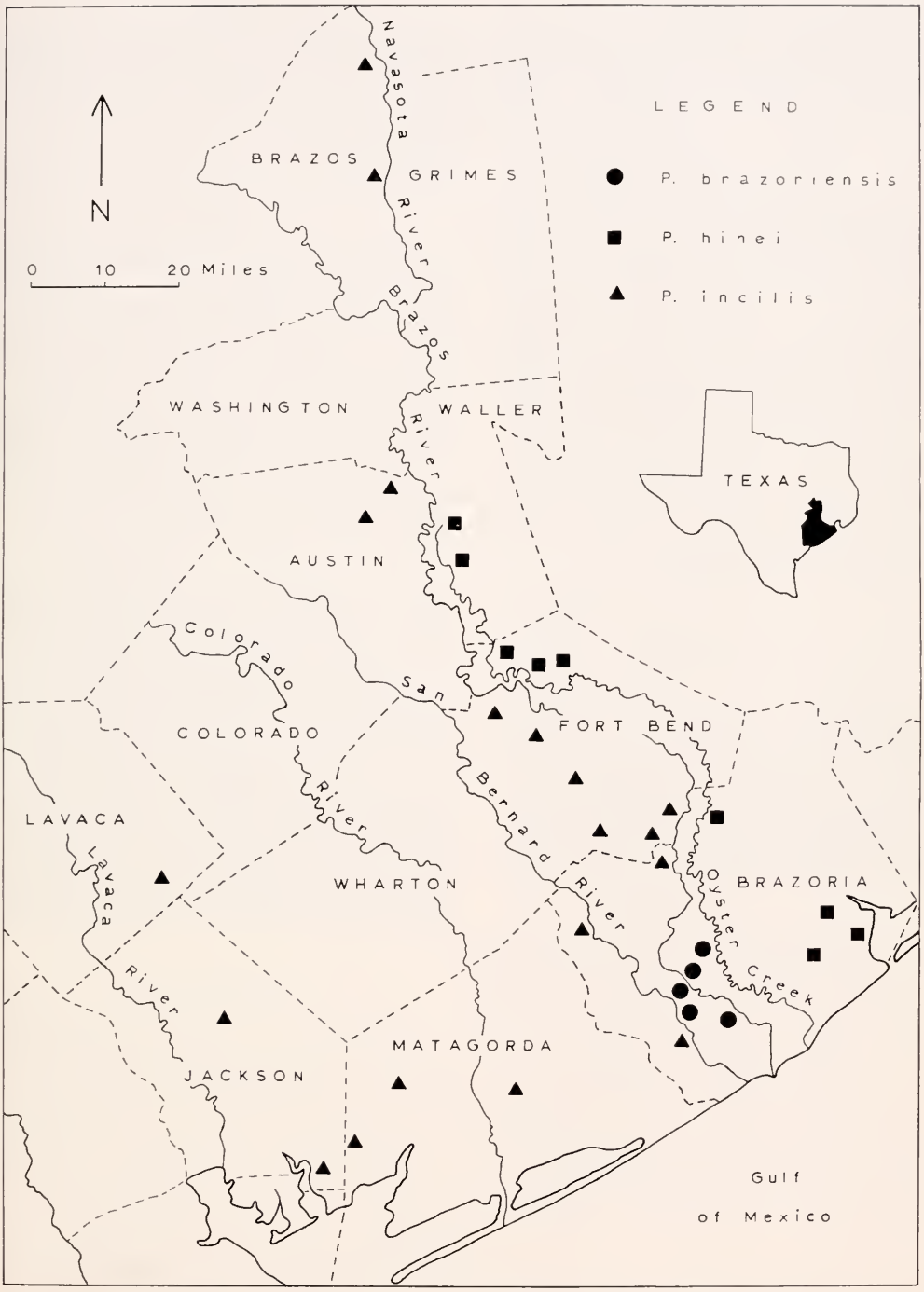

Figure 2. New distributional records for *Procambarus*, subgenus *Capillicambarus*, in Texas (eastern localities for *P. hinei* not included).

P. hinei and *P. incilis*, as might be suggested by its occurrence between the ranges of the latter two species. The annuli ventrales of females of the three species are virtually indistinguishable. Statements that *P. hinei* and *P. incilis* have immovable annuli ventrales (Penn, 1953, 1962) are erroneous.

Procambarus brazoriensis differs from *P. hinei* in having the apical third of the pleopod expanding distally in mesial view and ending abruptly, not tapering to its apex as in *P. hinei*. The cephalic process is wider than that of *P. hinei* both at the base and at its truncate tip, and lies in a more nearly longitudinal plane (with respect to the axis of the animal). The cephalic process of *P. hinei* is nearly transverse in orientation.

Life history notes.—Form I males have been present in every month for which collections are available: March, June, July, August, and September. Large numbers of small young were present in June. Females had sperm plugs in March and August.

Distribution of *Procambarus hinei* (Ortmann)

This species has a spotty distribution throughout most of Louisiana west of the Mississippi River, and in the southeastern corner of Texas. Penn (1956) recorded it from 12 parishes in Louisiana. Previous Texas records are from Harris, Liberty, and Jefferson Counties (Penn and Hobbs, 1958). I have collected it at 16 localities in Texas, as far west as the Brazos River (Fig. 2).

Collection Localities: Brazoria County—2.3 mi. W Rosharon (DWA T12-5), 5 mi. S Danbury (DWA 438), 6.5 mi. SE Danbury (DWA T13-5), 11 mi. SE Danbury (DWA 362); Fort Bend County—2 mi. NW Fulshear (DWA T9-1), 1.6 mi. E Fulshear (DWA T9-7), 5.3 mi. E Fulshear (DWA 432); Jasper County—6 mi. S Evadale (DWA 398); Liberty County—4.8 mi. NW Moss Hill (DWA 403), 0.7 mi. W Moss Hill (DWA 402), 2 mi. E Liberty (DWA 404), 3.3 mi. N Hull (DWA 401); Newton County—15 mi. N Deweyville (DWA 396), 7.8 mi. N Deweyville (DWA 395); and Waller County—9 mi. SSE Hempstead (DWA T7-2), 11 mi. NNW Brookshire (DWA T7-3, T7-4, T7-6).

One of J. B. Black's collections (JBB 145, 1 mi. NE Brazoria, Brazoria County) from the range of *P. brazoriensis* contains a single first form male *P. hinei* in addition to several *P. brazoriensis*. Sympatric occurrence of the two species would be quite significant. However, subsequent collecting at that locality has produced only *P. brazoriensis*, and I am reluctant to accept a record based on one specimen, fearing the possibility of error.

Distribution of *Procambarus incilis* Penn

Previously recorded from Jackson, Matagorda, and Wharton Counties, Texas (Penn, 1962). These localities, and more recent additional collecting, suggest that its range (Fig. 2) is bounded on the southwest by the Lavaca River and Bay. To the east, it appears to be separated from *P. brazoriensis* by the lower San Bernard River, and from *P. hinei* by the Brazos River north almost to its confluence with the Navasota River. *P. incilis* has been collected by the author or by J. B. Black at 19 localities.

Collection Localities: Austin County—3.8 mi. NE Belleville (DWA T8-1), 7.8 mi. NE Belleville (DWA T8-4); Brazoria County—1.7 mi. E Danciger (DWA 418), 7 mi. E Damon (DWA 410), 7 mi. S Brazoria (DWA T14-3); Brazos County—7 mi. NE Kurten (DWA 383), 8 mi. E College Station (DWA T4-2, T4-4); Fort Bend County—10.5 mi. W Rosenberg (DWA T10-5), 4.5 mi. W Rosenberg (DWA T10-2), 7 mi. S Rosenberg (DWA 431), 6.3 mi. E Needville (DWA T11-1), 13.5 mi. ESE Needville (DWA T11-5), 15.5 mi. E Needville (DWA T11-2); Jackson County—5 mi. NE Edna (JBB 421), 8.5 mi. W Palacios (JBB 153); Lavaca County—4 mi. N Speaks (DWA 437); and Matagorda County—8 mi. NW Palacios (DWA T16-6), 1.5 mi. E Blessing (DWA T16-5), 3 mi. N Wadsworth (DWA T15-7).

Zoogeography

The range of *Procambarus brazoriensis* appears to be separated from that of *P. incilis* to the southwest by the San Bernard River, and from that of *P. hinei* to the northeast by Oyster Creek (Fig. 2). Extensive collecting around the periphery of the range has failed to disclose intergrades, or to close the gap between *P. brazoriensis* and its relatives to the north and northwest. The single record of *P. hinei* occurring together with *P. brazoriensis* may be indicative of a sparse population of *P. hinei* existing sympatrically with *P. brazoriensis*, attesting their specific status relative to one another.

The present delimitation of the range

largely by rivers might suggest that these streams isolated a segment of the parental stock, which diverged to become *P. brazoriensis*. However, the geological events leading to the present situation are much too recent for such an explanation to be tenable. This area lies on the Brazos-Colorado alluvial plain, which is of Recent origin. Development of the Oyster Creek course, formerly occupied by the Brazos River, and establishment of the modern lower Brazos have occurred in the last 2,000–4,000 years (Bernard, LeBlanc, and Major, 1962). Late in the Pleistocene the lower Brazos lay west of its present course.

Major rivers may have been important in the derivation of *P. brazoriensis*, but probably it formerly occupied a larger range. Later changes in stream courses may have divided its range, with isolated populations subsequently becoming extinct. A possible explanation for the loss of such populations is the disappearance of barriers separating them from their close relatives, with which they were unable to compete or into the populations of which they were assimilated (if capable of interbreeding). Perhaps survival of members of the subgenus continues to depend, to a degree, on the partial isolation from one another afforded by the rivers separating their ranges.

Further evidence that *P. brazoriensis* was derived from *P. hinei* (or vice versa) rather than from *P. incillis* can be seen in the distribution of the small crawfish, *Cambarellus puer*. *C. puer* occurs together with *P. brazoriensis* and *P. hinei* throughout their ranges, but is not found in the range of *P. incilis* (with two known exceptions in Brazoria County, both localities probably recently colonized).

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A NEW TROGLOBITIC CRAYFISH OF THE GENUS *PROCAMBARUS* FROM FLORIDA (DECAPODA: ASTACIDAE)

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ABSTRACT

A new troglobitic crayfish of the genus *Procambarus* is described from northern Florida. The new crayfish is most closely related to *P. lucifugus lucifugus* and *P. lucifugus alachua*. The Florida troglobitic crayfishes are illustrated, and a key to them is presented.

Only a year ago, the description of a new troglobitic crayfish, *Procambarus milleri* Hobbs (1971), from Dade County Florida, appeared. Suspecting that it was probably the last undescribed troglobitic crayfish occurring in the State, Hobbs presented a key to the seven species and subspecies that were known at that time and illustrated certain of their diagnostic features. After that manuscript had been accepted for publication, adult specimens of the crayfish from Leon and Wakulla counties that he had tentatively identified (loc. cit., p. 123) as *Procambarus pallidus* (Hobbs, 1940), were obtained by D. Bruce Means, and specimens of another troglobite were collected in Jefferson County by Michael N. Horst. Both proved to be distinct and were described by Hobbs and Means (1972).

In the meantime, Frank Redmon had discovered the sinkhole that is here designated the type-locality of the new species described below, and in November, 1971, Frank Hurt collected the first specimens of this species, one of which is being maintained alive in the Jacksonville Children's Museum. Additional specimens, including the holotypic male, were collected by him and Barry W. Mansell on November 23, 1971. Except for the holotype, all of the specimens on which the following description is based were obtained in January and February 1972 by the authors.

In order to provide a comparable series of illustrations of all of the Floridian troglobitic crayfishes, Figures 2–4 are included to complement those of the seven species and subspecies figured in Hobbs, 1971. A revised key to these troglobites is also presented.

We extend our appreciation to Frank Hurt and Barry W. Mansell who first collected the crayfish described herein and who have permitted us to prepare this account of it. We are deeply indebted to Dr. Horton H. Hobbs, Jr., Smithsonian Institution, who actually prepared the bulk of the description of the new species and the Figures, and who has kindly allowed publication in this paper of his revised key to the troglobitic crayfishes. This contribution to science is as much his as ours.

Procambarus (*Ortmannicus*) ***erythrops***, new species

Diagnosis: Integument white to pale tan; eyes moderately small, lacking facets, but with conspicuous red pigment spot. Rostrum with marginal spines. Areola 8.3 to 14.5 times longer than wide and comprising 35.3% to 38.7% of entire length of carapace (45.3% to 48.1% of postorbital length). Single pair of cervical spines present. Suborbital angle absent. Postorbital ridges terminating cephalically in a spine and several tubercles at caudal base. Hepatic area of carapace with crowded tubercles, some spiniform. Antennal scale approximately 1.7

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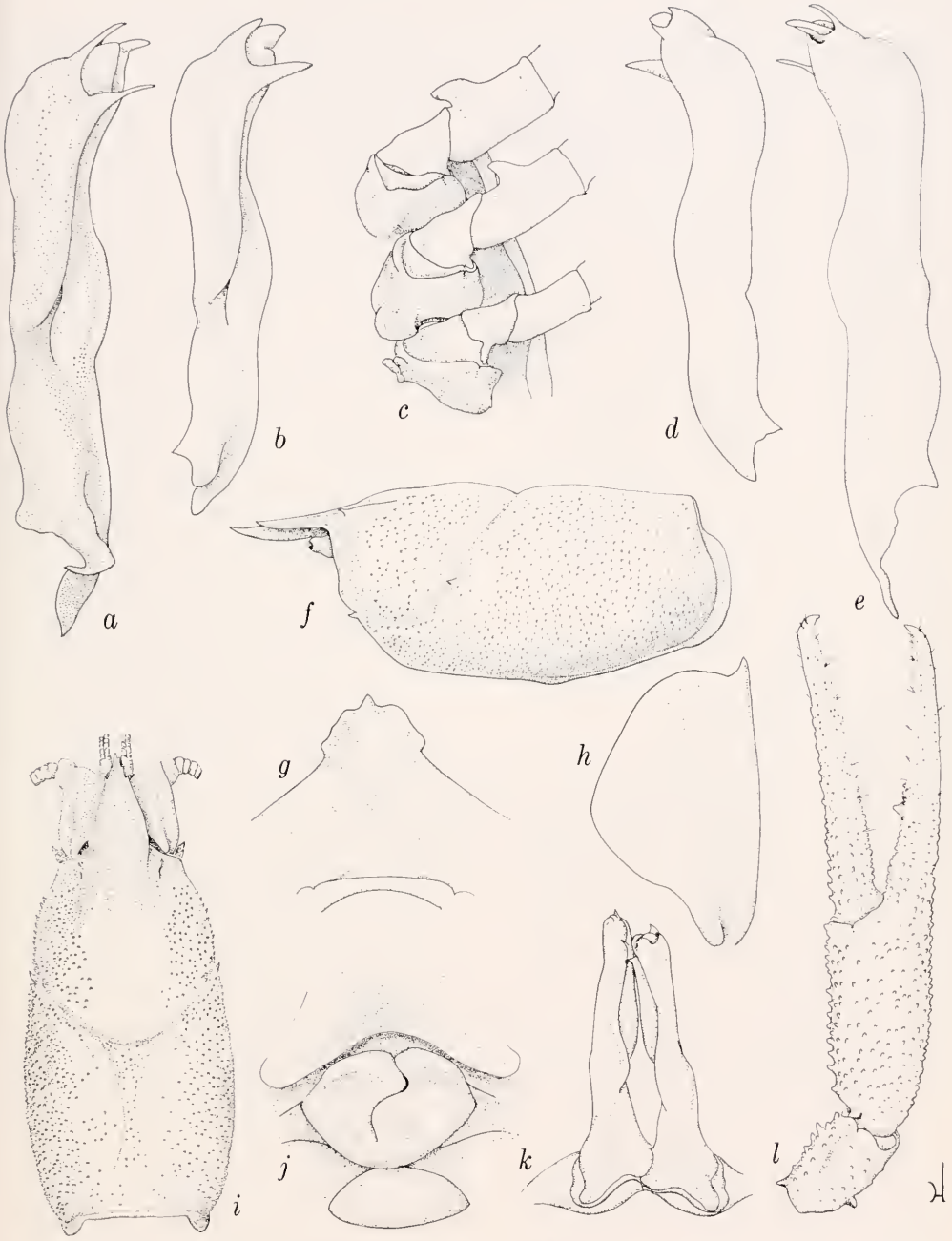


Figure 1. *Procambarus erythrops*, new species. *a*, Mesial view of first pleopod of holotype; *b*, Mesial view of first pleopod of paratypic male, form II; *c*, Basal podomeres of third, fourth, and fifth pereiopods of holotype; *d*, Lateral view of first pleopod of paratypic male, form II; *e*, Lateral view of first pleopod of holotype; *f*, Lateral view of carapace of holotype; *g*, Epistome of holotype; *h*, Antennal scale of holotype; *i*, Dorsal view of carapace of holotype; *j*, Annulus ventralis of allotype; *k*, Caudal view of first pleopods of holotype; *l*, Dorsal view of distal podomeres of cheliped of holotype.

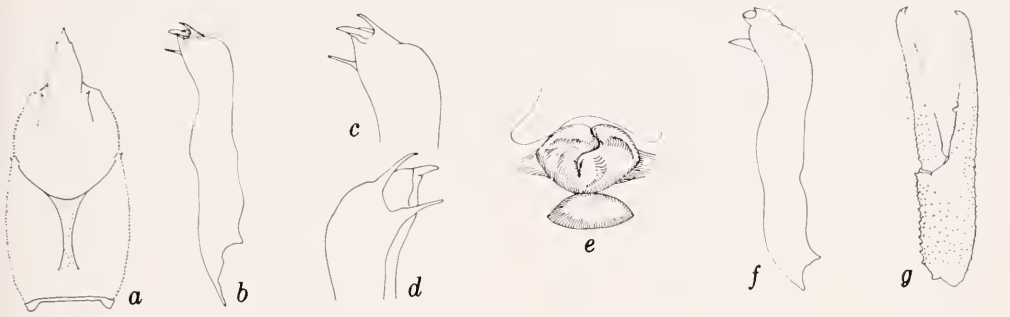
times longer than wide, widest proximal to midlength. Ischia of third and fourth pereiopods with hooks, that on third overreaching basioischial articulation. First pleopods asymmetrical, with distinct rounded hump on cephalic surface, subapical setae, and reaching cephalically to coxae of third pereiopods; distal extremity bearing (1) subspiculiform mesial process directed caudodistally and slightly laterally; (2) prominent, slender, acute cephalic process cephalic to and partially hooding central projection, directed caudodistally; (3) corneous, long central projection extending caudodistally at 75° to 80° to main shaft of appendage and almost as far caudally as mesial process, and (4) caudal element consisting of prominent crestlike adventitious ridge (process) situated mesial to central projection; caudal knob and caudal process absent. Annulus ventralis with cephalolateral margins elevated (ventrally) and with raised caudomedian prominence; sinus originating on cephalic margin, and, following sinuous contour, ending on caudomedian prominence. Sternum immediately cephalic to annulus entire, lacking caudally projecting prominences and tubercles.

Holotypic Male, Form I: Body (Fig. 1*f,i*) subcylindrical. Eye reduced in size, lacking facets but provided with small red pigment spot. Abdomen narrower than thorax (16.0 and 21.1 mm, respectively). Width of carapace greater than height at caudodorsal margin of cervical groove (21.3 and 18.0 mm). Areola 10.0 times longer than wide with one or two punctations across narrowest part. Cephalic section of carapace about 1.7 times longer than areola; length of areola 37.3% of entire length of carapace (47.1% of postorbital length). Rostrum excavate dorsally with unthickened, convex margins interrupted by paired marginal spines at base of acumen, latter reaching level of distal end of peduncle of antennule and bearing two accessory spines on dextral margin and two smaller ones on sinistral margin; setiferous punctations arranged in submarginal row and few scattered over remainder of surface of rostrum, most abundant at level of orbit. Subrostral ridges rather weak, not evident in dorsal aspect except in caudalmost portion of orbit. Postorbital ridges clearly defined, with acute, curved spines cephalically and few small tubercles caudally; dorsolateral groove shallow, inconspicuous. Suborbital angle absent. Branchiostegal spine prominent, acute. Dorsomedian portion of carapace sparsely punctate; hepatic region tuberculate except cephalically, some tubercles acute or spiniform; branchiostegites thickly studded with tubercles, especially cephaloventrally; only one cervical spine present on each side although part of a series of small acute tubercles along caudal flank of cervical groove.

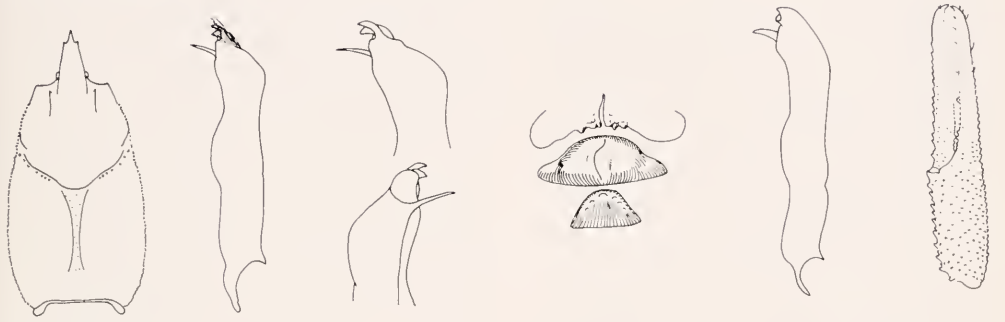
Abdomen shorter than carapace (44.0 and 45.6 mm). Cephalic section of telson with three spines in each caudolateral corner, mesial two movable. Cephalic lobe of epistome (Fig. 1*g*) with convergent, somewhat thickened, ventrally elevated, undulating cephalolateral margins; subtruncate cephalic margin bearing acute median projection; basal portion with median longitudinal depression, lacking distinct fovea. Antennules of usual form with prominent distally directed spine near midlength of ventral surface of basal article of peduncle. Antennae exceeding caudal margin of telson by length slightly greater than that of carapace. Antennal scale (Fig. 1*b*) 1.7 times longer than broad with greatest width distinctly proximal to midlength, lamellar area about 2.5 times broader than thickened lateral part, latter terminating in strong, short spine.

Third maxillipeds extending anteriorly to level of tip of rostrum; opposable margin of ischium with teeth, its lateral surface serrate distally; ventral surface almost naked, but mesioventral surface with several sublinear series of stiff, long setae.

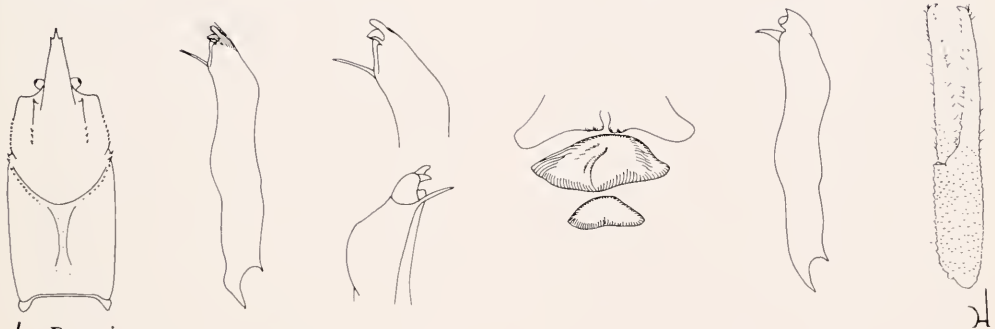
Right chela (Fig. 1*l*) slender, subovate in cross section, not strongly depressed. Mesial surface of palm with tubercles not distinctly arranged in linear series but with 10 or 11 in relatively straight line and additional ones above and below; lateral margin of palm with serrations extending to distal end of proximal third of fixed finger; dorsal and ventral surfaces of both fingers with submedian longitudinal ridges flanked proximally by conspicuous tubercles, distally by setiferous punctations. Fixed finger with row of 15 tubercles along proximal two-fifths; with distinctly larger, corneous-tipped tubercle on lower level (between twelfth



2. P. erythrops



3. P. horsti



4. P. orcinus

Figures 2–4. Floridian troglobitic crayfishes. *a*, Dorsal view of carapace; *b*, Lateral view of left first pleopod of first form male; *c*, Mesial view of distal portion of same; *d*, Lateral view of distal portion of same; *e*, Annulus ventralis; *f*, Lateral view of left first pleopod of second form male; *g*, Dorsal view of chela of first form male.

and thirteenth tubercle from base) followed immediately distally by two additional progressively smaller tubercles; band of crowded minute denticles beginning between rows at level of large tubercle, broadening distally, extending almost to corneous tip of finger. Opposable margin of dactyl with row of 12 tubercles extending from base almost to level of major tubercle on fixed finger, with row of seven tubercles beginning dorsal to, and between, two distalmost tubercles in latter row, ending at level immediately proximal to distalmost tubercle of row on fixed finger; tubercles of both rows decreasing in size distally, band of crowded minute denticles as on fixed finger; mesial surface of dactyl with tubercles extending from proximal portion to base of distal one-fourth of finger.

Carpus of right cheliped longer than broad

Table 1. Measurements (mm) of *Procambarus (Ortmannicus) erythrops*.

	Holotype	Allotype	Morphotype
Carapace:			
Height	18.0	14.3	18.0
Width	21.1	16.1	20.0
Length	45.6	34.8	42.7
Areola:			
Width	1.7	1.5	1.3
Length	17.0	12.9	16.0
Rostrum:			
Width	5.9	4.5	5.5
Length	11.9	8.3	10.6
Right Chela:			
Length of mesial margin of palm	15.0	10.5	14.9
Width of palm	8.9	6.0	8.2
Length of lateral margin of chela	41.5	28.6	42.1
Length of dactyl	25.1	17.4	25.3

(10.3 and 6.0 mm), with all surfaces tuberculate; dorsal surface with distinct oblique furrow; dorsomesial surface with row of three tubercles, distalmost distinctly larger than others nearby; largest tubercle on podomere situated on distal ventromesial border; additional strong tubercle on ventrodistal condyle.

Merus of right cheliped tuberculate except for proximal portion of mesial and lateral surfaces; dorsal surface with crowded tubercles, more numerous distally, largest subspiniform and situated subapically; ventral surface with sublinear series of 20 tubercles mesially, less well defined row of 14 laterally; additional tubercles between and flanking both rows; distal ventrolateral angle with strong, spiniform tubercle. Ischium with tubercles dorsally and ventrally, five larger ones linearly arranged along ventromesial margin. Basis with single tubercle in position corresponding to ventromesial row of tubercles on ischium (two on left cheliped).

Hooks on ischia of third and fourth pereiopods (Fig. 1*c*) simple, that on third overreaching basioischial articulation, that on fourth not reaching corresponding articulation, not opposed by tubercle on basis. Coxa of fourth pereiopod with prominent, swollen caudomesial boss, that of fifth with small tuberculiform prominence extending caudomesially and somewhat ventrally from caudomesial angle.

Sternum between second, third, and fourth pereiopods rather deep, ventrolateral margins bordered with long setae.

First pleopods (Fig. 1*a,e,k*) as described in diagnosis. In addition, subterminal setae arising around base of cephalic process and along lateral base of central projection, completely obscuring both processes in lateral aspect.

Uropod with distally directed spine on each basal lobe; median spine on mesial ramus not nearly reaching distal margin of ramus.

Allotypic Female: Differing from holotype in following respects: acumen without accessory spines; punctations on dorsal surface of rostrum at level of orbit few, most lacking setae; cephalic section of telson with only two spines in each caudolateral corner; cephalic margin of cephalic lobe of epistome more deeply emarginate on each side of median projection; tubercles on mesial margin of palm of chela more nearly linearly arranged, mesialmost row consisting of 11 or 12; opposable margin of both fingers of chela with row of 12 tubercles, fixed finger with usual additional large tubercle on lower level, but with additional two on holotype lacking; carpus of cheliped with three large spines on distal margin, two ventral ones as described in holotype, and one mesial to dorsal articular knob; merus with several distinctly spiniform tubercles on dorsodistal surface, ventral surface with one or two more tubercles in each of two poorly defined rows; ischium with tubercle on ventromesial margin virtually obsolete.

Annulus ventralis (Fig. 1*j*) not deeply embedded in sternum, subovate, broader than long with cephalic margin elevated ventrally, bearing median emargination marking origin of sinus; latter extending caudally in form of tilted, reversed "S," ending sinistral to median line on submedian elevation near caudal margin of annulus. Sternum immediately cephalic to annulus without caudally projecting prominences or tubercles. Postannular plate much broader than long, only little narrower than width of annulus, its

width, however, greater than greatest length of annulus.

Morphotypic Male, Form II.—Differing from holotype in following respects: acumen of rostrum lacking accessory spines; lateral surface of fixed finger of cheliped with serrations extending to midlength of finger; opposable margin of dactyl with row of 18 tubercles in single row; irregular row of 15 or 16 tubercles on ventrolateral surface of merus; ventromesial surface of ischium with row of six tubercles on left cheliped, corresponding basis lacking tubercle; basis of right cheliped with one tubercle mesially. Hooks on ischia of third and fourth pereiopods distinctly reduced, neither reaching basioischial articulation; prominences on coxae of fourth and fifth pereiopods not conspicuously smaller than those in holotype.

First pleopods strongly asymmetrical with few subapical setae, as depicted in Fig. 1*b,d*. Mesial and cephalic processes and central projection much more robust than in holotype; caudal element represented by tumescence at caudomesial base of central projection.

Type-locality: Sim's Sink, 1 mi west of the junction of U.S. Hwys. 27 and 129, and 0.1 mi south of Hwy. 27, Suwannee County, Florida (Sec. 24, T. 6S, R. 14E). The shallow, funnel-shaped sink reaches ground water at a depth of approximately 12 feet. The original owners have partially covered it with boards upon which there is an accumulation of detritus, mosses, and ferns, but broken portions of the roof and spaces between boards allow detritus to filter into the sinkhole. The pool of water is elliptical, measuring approximately 8 by 12 feet, and is bounded by a nearly vertical shaft of limestone for half of its circumference to a depth of about 30 feet (bottom of pool). There are small ledges and crevices in the limestone wall. Opposite the vertical wall, the pool opens to a cave of unknown extent, and during periods of lower water levels, the surface area of the pool is greater since part of the ceiling of the cave is then above the water. *Procambarus erythrops* occurs throughout the sink and explored cave area.

Types: The holotypic male, form I, allotypic female, and morphotypic male, form II (Nos. 133471, 133472, and 133473 respectively) are deposited together with paratypes (4♂I, 3♂II, 8♀, 6 juv.♂, 1 juv.♀) in the National Museum of Natural History, Smithsonian Institution. An additional series of paratypes (1♂I, 1♂II, 1♀) are in the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

Range: *Procambarus erythrops* is known to occur in only two localities in Suwannee County, Florida. The location of the type-locality is cited above, and the other is an unnamed sink situated only 0.2 mi south of it.

Variations: The more conspicuous variations noted probably have resulted from regenerations of lost parts. For example, the multiple spines on the acumen of the holotype is unique among available specimens, and there is evidence that the acumen was injured in an earlier instar. The usual minor differences in the arrangement of spines and tubercles obtain, and, while not mentioned in the above descriptions, the opposable margins of the coxae of the chelipeds may bear zero to three spiniform tubercles that may or may not be symmetrically balanced or arranged. The range of variations in certain body proportions are cited in the Diagnosis, and certain secondary sexual differences are shown in Table 1. In addition, the setose ventrolateral margins of the sternum in the first form males contrast markedly with the sparse, short setae on the corresponding areas of the females and second form males.

Life History Notes: With the exception of the holotype, which was obtained on November 23, 1971, all specimens included in the type-series were collected on January 23 and February 25, 1972. First form males were obtained on all three dates. No ovigerous females or ones carrying young have been observed. Seven juveniles with carapace lengths ranging from 8.9 to 20.0 mm were among the two 1972 lots. Another troglobitic crayfish, *Troglocambarus maclanei*, is a coinhabitant of the type locality.

Size: The largest specimen available is the holotype that has a carapace length of 45.6 mm (postorbital length 36.1 mm). The smallest first form male has corresponding lengths of 36.8 and 29.3 mm, respectively.

Relationships: *Procambarus erythrops* is more closely allied to *P. lucifugus lucifugus*

(Hobbs, 1940) and *P. lucifugus alachua* (Hobbs, 1940) than to any other crayfishes, sharing with them not only albinistic qualities, but also a strongly tuberculate carapace and chelipeds, the latter slender and long. In the males, all of the secondary sexual characters are markedly similar, and in the females, not only are the annuli ventrales nearly identical but also the sternum immediately cephalic to the annulus is without tubercles or caudally projecting prominences. This crayfish may be distinguished from *P. l. lucifugus* most readily by the red eye spot and an areola less than 15 times longer than broad and usually constituting less than 38% of the total length of the carapace. It differs from *P. l. alachua* in having red instead of black pigment in the eye, convex rostral margins, and a stronger curvature of the distal portion of the first pleopod of the male. More distantly, it is related to *P. horsti*, *P. orcinus*, and *P. pallidus* from which the male can be distinguished by the hook on the ischium of the fourth pereiopod that does not overreach the basioischial articulation and which is not opposed by a tubercle on the basis; also, the terminal portion of the first pleopod is distinctly different having a longer central projection, and the cephalic process is never situated lateral to the central projection. The females of the latter three species all have tubercles on the caudal margin of the sternum immediately cephalic to the annulus ventralis, whereas, in *P. erythrops* this portion of the sternum lacks tubercles.

Procambarus erythrops resembles the two subspecies of *P. lucifugus* so closely that it could be designated a third subspecies of the complex. There are two reasons for considering it a full species: (1) we have no evidence of intergradation; and (2) *P. erythrops* shares much more in common with the nominate species than with *P. l. alachua*, its geographically closer relative. Only in possessing pigment in the eye does it resemble *P. l. alachua* more closely; even in this similarity, however, the pigment of *P. erythrops* is distinctly red whereas that of *P. l. alachua* is black. To our knowledge, only one other crayfish, *P. orcinus*, has red pigment in its eyes, but in no other respect does it approach *P. erythrops* as closely as do the two subspecies of *P. lucifugus*.

Etymology: Erythros (G., red) + Ops (G., eye); alluding to the red pigment spot in the eye of this crayfish.

Key to the Troglobitic Crayfishes of Florida

By Horton H. Hobbs, Jr.

(Modified from Hobbs, 1971. The subgeneric designations are those treated by Hobbs 1969, 1972)

1 Third maxillipeds lacking teeth on opposable border of ischium ..... *Troglocambarus maclanei* Hobbs, 1942. (Caves from Citrus and Hernando to Suwannee Counties)

1′ Third maxillipeds with teeth on opposable border of ischium 2

2 Male with hooks on ischia of third pereiopods only; first pleopod with two terminal elements bent at right angles to main shaft of appendage. Female with annulus ventralis fused to sternum immediately cephalic to it ... *Cambarus* (*Jugicambarus*) *cryptodytes* Hobbs, 1941. (Caves and well in Jackson County, Florida and Decatur County, Georgia)

2′ Male with hooks on ischia of third and fourth pereiopods; first pleopod with more than two terminal elements and never with all bent at right angles to main shaft of appendage. Female with distinct flexible membrane separating annulus ventralis from sternum immediately cephalic to it, or membrane obscured by multituberculate processes projecting caudally from sternum 3

3 Eye with pigment spot 4

3′ Eye without pigment 7

4 Pigmented area of eye with facets; rostrum without marginal spines or tubercles. Male with first pleopod bearing distally directed mesial process. Female unknown ..... *Procambarus* (*Leconticambarus*) *milleri* Hobbs, 1971. (Well in Dade County)

4′ Pigmented area of eye without facets; rostrum with marginal spines or tubercles. Male with first pleopod

bearing caudally or caudodistally directed mesial process 5

5 Pigment spot in eye black. Areola more than 20 times longer than broad ..... *Procambarus* (*Ortmannicus*) *lucifugus alachua* (Hobbs, 1940). (Caves and sinkholes in Alachua and Gilchrist counties)

5′ Pigment spot in eye red. Areola less than 20 times longer than broad 6

6 Male with hook on ischium of fourth pereiopod reaching basioischial articulation and opposed by tubercle on basis; cephalic process of first pleopod situated lateral to central projection. Female with caudally directed tuberculiform prominences on caudal margin of sternum immediately cephalic to annulus ventralis ..... *Procambarus* (*Ortmannicus*) *orcinus* (Hobbs and Means, 1972). (Springs and sinkholes in Leon and Wakulla counties)

6′ Male with hook on ischium of fourth pereiopod not reaching basioischial articulation and not opposed by tubercle on basis; cephalic process of first pleopod situated cephalic to central projection. Female without caudally directed tuberculiform prominences on caudal margin of sternum immediately cephalic to annulis ventralis ..... *Procambarus* (*Ortmannicus*) *erythrops*, new species (Sinkholes in western Suwannee County)

7 Male with hooks on ischia of third and fourth pereiopods bituberculate; first pleopod lacking subapical setae, and cephalic and mesial processes directed distally. Female with annulus ventralis at least as long as broad ..... *Procambarus* (*Lonnbergius*) *acherontis* (Lönnberg, 1895). (Spring and well in Seminole County)

7′ Male with hooks on ischia of third and fourth pereiopods simple; first pleopod with subapical setae, and cephalic and mesial processes directed caudally or caudodistally. Female with annulus ventralis shorter than broad 8

8 Rostrum narrower at base than along orbit. Male with central projection of first pleopod narrow and elongate; hook on ischium of fourth pereiopod not reaching basioischial articulation. Female without caudally directed tubercles on caudal margin of sternum immediately cephalic to annulus ventralis ..... *Procambarus* (*Ortmannicus*) *lucifugus lucifugus* (Hobbs, 1940). (Caves from Citrus and Hernando counties northward to Marion County where it intergrades with *P. l. alachua*)

8′ Rostrum tapering from base. Male with central projection of first pleopod beaklike; hook on ischium of fourth pereiopod overreaching basioischial articulation. Female with caudally directed tubercles on caudal margin of sternum immediately cephalic to annulus ventralis 9

9 Postorbital ridges with caudally situated spines or tubercles; areola less than 20 times longer than broad. Male with cephalic process of first pleopod situated lateral to central projection ..... *Procambarus* (*Ortmannicus*) *horsti* Hobbs and Means, 1972. (Well and spring in Jefferson and Leon counties)

9′ Postorbital ridges without caudally situated spines or tubercles; areola more than 20 times longer than broad. Male with cephalic process of first pleopod situated cephalic to and partially hooding central projection ..... *Procambarus* (*Ortmannicus*) *pallidus* (Hobbs, 1940). (Caves and sinkholes in Alachua, Columbia, and Suwannee counties)

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A NEW CRAWFISH OF THE GENUS *ORCONECTES* FROM CONCHAS LAKE, NEW MEXICO[1]

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ABSTRACT

Orconectes deanae is described from Conchas Lake, South Canadian River drainage, in San Miguel County, New Mexico. It is most closely related to members of the Palmeri Group of the Virilis Section.

The species described herein has been known to the authors since 1960 but a lack of sufficient material to base our description (2 Form I males; 1 female) has prevented us from describing it until now. Recently a fine series of Form I males was collected at Conchas Lake, the type locality, resulting in this description.

Orconectes deanae is closely related to members of the Palmeri Group of the Virilis Section but can easily be distinguished from all other *Orconectes* by differences in the first pleopods of Form I males and the annulus ventralis of females.

The authors wish to express their appreciation to Dr. Horton H. Hobbs, Jr. for his helpful advice and review of this paper.

Orconectes ***deanae*** new species
(Figures 1–8)

Orconectes causeyi Jester, 1967, pp. 518, 521, 523 (in part).

Diagnosis.—Rostrum with distinct acumen and lateral spines; without carina. Areola obliterated, constituting 30.6% to 33.7% (average 32.1%) of entire carapace length. Chelae as in other species of Palmeri Group. First pleopod of Form I male terminating in two strongly bent rami, reaching coxopodite of second pereiopods when abdomen flexed. Central projection of first pleopod bent at approximately 45° angle and representing 20.5% to 23.8% (average 23.0%) of entire pleopod length; mesial process bent at approximately 90° angle and 19.3% to 22.1% (average 21.2%) of entire pleopod length.

Holotypic male Form I.—Body pigmented; eyes normal. Body subcylindrical, only slightly depressed. Abdomen narrower than carapace (16.7 mm and 20.0 mm in widest parts, respectively).

Rostrum reaching distal podomere of peduncle of antennule; margins subparallel, slightly thickened, terminating cephalically in tubercles; excavate dorsally; carina absent; acumen 32.7% length of entire rostrum. Postorbital ridges strong, each with prominent groove, terminating cephalically in prominent spine. Areola obliterated. Cephalic section of carapace 1.96 times as long as thoracic section. Suborbital angle absent. Branchiostegal spine acute. One prominent cervical spine on each side of carapace (additional small spine on left side, dorsal to prominent spine) just caudal to cervical groove. Carapace with setiferous punctations

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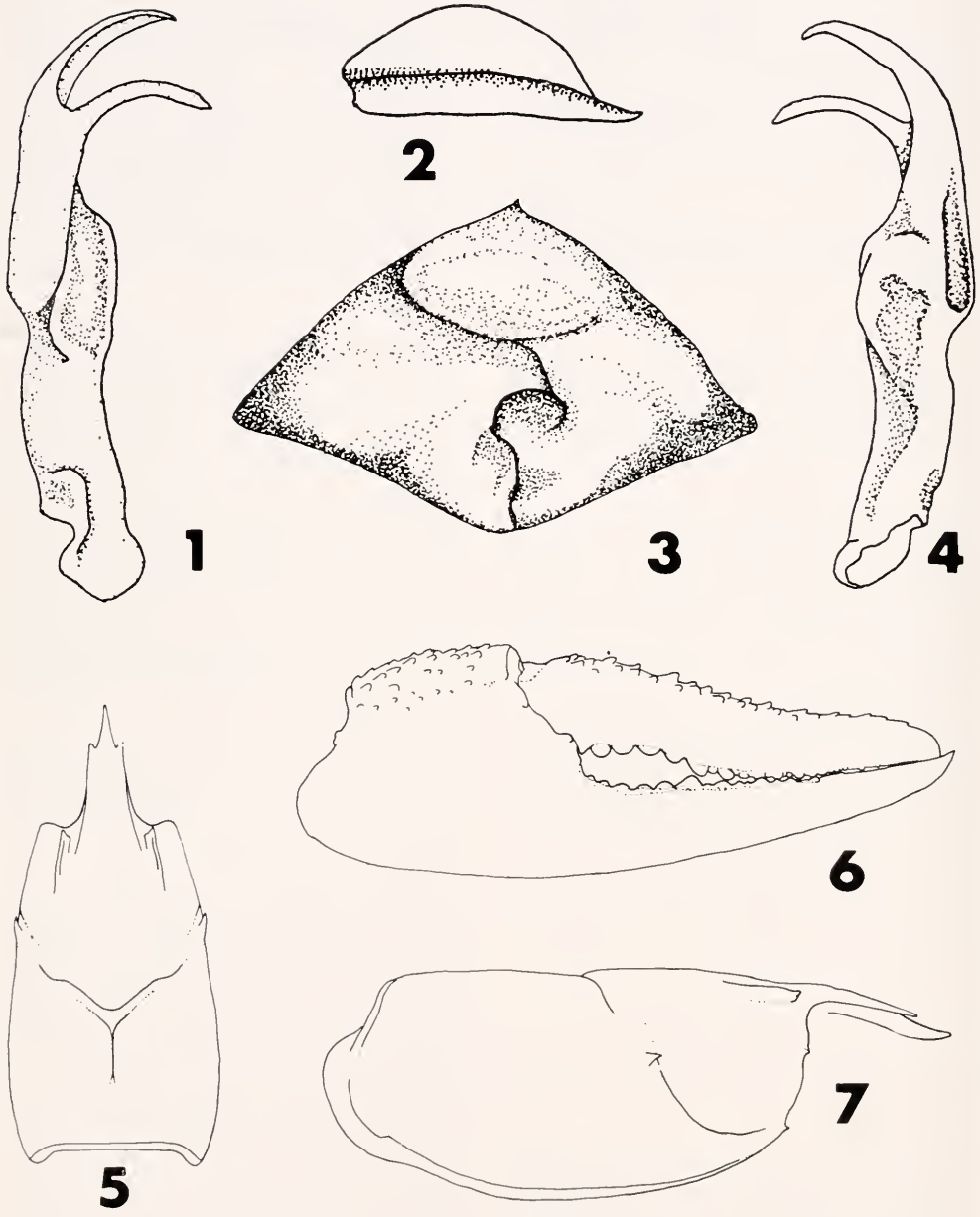

Figures 1–7. *Orconectes deanae* n. sp.: 1, mesial view of first pleopod of paratypic Form I male; 2, antennal scale; 3, annulus ventralis of paratypic female; 4, lateral view of first pleopod of paratypic Form I male; 5, dorsal view of cephalothorax of holotype; 6, right chela of holotype; 7, lateral view of cephalothorax of holotype.

dorsally and caudolaterally, becoming setiferous squamous tubercles cephalolaterally. Carapace wider than high in region of caudodorsal margin of cervical groove (20.0, 16.4 mm, respectively).

Length of abdomen subequal to that of carapace (40.0, 41.6 mm, respectively). Cephalic section of telson with two prominent spines on each caudolateral corner.

Epistome subcircular in outline; with ele-

Table 1. Measurements of portion of type-series (in millimeters).

	Holotype[1]	Allotype[2]	Form I males								
Carapace											
Height	16.4	13.9	16.2	15.2	13.8	14.8	13.5	15.1	10.3	10.5	12.6
Width	20.0	15.8	19.4	18.7	16.7	17.8	16.5	17.0	12.9	13.0	15.8
Length	41.6		41.5	38.6	35.0	37.4	35.0	36.4	27.8	27.8	32.5
Cephalic length	27.6		28.3	26.8	23.8	25.1	24.0	24.5	18.7	19.0	22.2
Areola length	14.0	10.8	13.1	11.8	11.2	12.3	11.0	11.9	9.1	8.8	10.3
Rostrum											
Length	10.4		11.9	11.1	9.8	10.0	10.3	10.0	8.3	8.0	9.3
Width	5.4	4.1	4.7	5.0	4.2	4.8	4.5	4.4	3.7	3.6	3.9
Acumen length	3.4		4.3	4.2	3.5	3.5	3.5	3.3	3.1	3.0	3.3
Chela, right											
Height	15.7	7.8	12.5	12.5	11.3	12.4	9.7	10.6	7.5	7.6	8.9
Palm-											
inner margin	11.6	5.1	7.5	8.5	8.5	9.1	6.7	7.5	5.6	5.6	5.9
outer margin	44.1	23.4	36.9	36.8	31.0	34.7	29.5	32.1	20.3	21.5	26.7
width	9.7	4.8	6.9	7.3	6.8	7.8	5.9	6.5	4.5	4.7	5.3
Dactyl length	29.3	16.5	25.9	25.2	20.9	23.3	20.6	22.5	13.6	14.6	19.0
Gonopod											
Length	11.6		11.1	10.4	10.0	10.5	10.1	10.2	8.4	8.3	10.0
Central projection length	2.4		2.6	2.4	2.3	2.4	2.2	2.4	2.0	1.7	2.3
Mesial process length	2.3		2.4	2.3	2.1	2.3	2.1	2.2	1.8	1.6	2.2
Antennal scale											
Length	9.2	8.4	9.1	8.7	8.5	8.6	8.3	8.7	7.0	7.0	8.5
Width	3.4	3.2	3.7	3.3	3.2	3.2	3.2	3.2	2.6	2.6	3.0
Abdomen											
Length including telson	40.0	33.9	40.3	36.3	36.0	36.4	34.2	37.1	27.7	27.3	32.7

[1] Distal projection of antennal scale broken.
[2] Acumen broken off even with lateral rostral spines.

vated margins; lacking cephalomedian protuberance.

Antennules with prominent spine on basal segment. Antennae normal, reaching to proximal half of telson. Antennal scale moderately broad terminating cephalically in strong acute spine; lamellar portion widest at mid-length.

Chelae with setiferous punctations above and below; outer margin not costate. Inner margin of palm with two rows of cristiform tubercles, upper row of eight, lower of nine; finger with slight gape, opposable margin of immovable finger with proximal row of six tubercles gradually increasing in size distally, followed by alternating small and large tubercles to distal ⅔; one tooth on inner surface at distal ⅔ followed by smaller tooth on same surface ½ distance between it and corneous tip; crowded minute denticles on distal ⅓, corneous tip overlying corneous tip of movable finger. Dactyl with two rows of tubercles along mesial margin; opposable margin with row of five subequal tubercles along proximal ⅓, followed by alternating small and large tubercles to level of last tubercle on opposable surface of immovable finger; minute denticles on distal ½.

Carpus longer than broad, with oblique furrow on upper surface; few scattered setiferous punctations above and below. Mesial surface with two tubercles on proxomesial margin; strong acute spine slightly distal to mid-length. Lower distolateral margin with strong acute spine; lower distomesial margin lacking ornamentation.

Upper distal surface of merus with two acute spines and two small tubercles proximally; lower distal surface with two rows of equidistant spines terminating with strong spine distally. Hooks on ischiopodites of third pereiopods only; hooks strong, simple, extending to proximal margin of ischiopodite.

First pleopods symmetrical, extending cephalad to caudal margin of second pereiopods when abdomen flexed; bifid distally. Central projection corneous and bent at approximately 45° angle to main shaft. Mesial process noncorneous and bent at approximately 90° angle to main shaft.

Allotypic female.—The acumen and tips of the antennae of the allotype are broken off. It differs from the holotype in the following ways: there is one prominent cephalic spine on each side of the carapace with two smaller spines on the left side (one above and one below the major spine) and one smaller spine on the right side (below the major spine); there is a third, smaller spine medially on the cephalic section of the telson; the tubercles on the inner surface of the palm of the chelae are not in distinct rows.

The annulus ventralis is sub-elliptical, being wider (3.7 mm) than long (2.4 mm). The cephalic third is depressed around a cephalomedial elevation. The sinus originates on the sinistral side, at the caudal region of the cephalically depressed area and extends caudally in an "s" pattern to just past the median line where it makes a shallow bend to the mid-caudal margin.

Morphotypic male.—Unknown.

Variations.—Few significant variations were observed in the specimens examined by the authors. Although the holotype and allotype have accessory cervical spines, none of the other adults possess them. Two spines on each caudolateral corner of the cephalic section of the telson also seems to be the rule rather than that variation exhibited by the allotype. The arrangement and number of tubercles on the chelipeds vary slightly but only in the allotype are the tubercles on the inner margin of the chela not arranged in two discernable rows.

Type-locality.—Conchas Lake, located at the junction of the Conchas and South Canadian Rivers in San Miguel County, on State Road 104 approximately 32 miles NW of Tucumcari, New Mexico.

The dam was finished in 1939. The surface area is approximately 10,000 acres and the average depth 38.6 ft. Surface temperatures vary from approximately 36° to 82° F annually. The bottom is composed mostly of gravel, sand, and sandstone bedrock with silt being abundant only at the deltas which have formed at the mouths of the Conchas and South Canadian Rivers. *Orconectes deanae* has been collected on all bottom types except silt. The fish fauna in Conchas Lake is composed of 21 "warm-water" species, many of which are known to feed on *O. deanae.*

The types were collected from under rocks and along a rocky ledge on the southern shoreline of the lake. Most were taken as they darted from under rocks in the shallow areas (around 6 inches in depth) toward the deeper water.

Three individuals (2 Form I males and 1 adult female) were obtained from the lake on January 15, 1960. They were entangled in a gill net set on the bottom at a depth of 70 feet.

A series of juvenile individuals were collected in July of 1969 from the shoreline west of the rocky area. Here the water is shallow much farther off shore, and, at the time the collection was made, there was a large area of inundated vegetation. No adults were seen.

Disposition of types.—The holotype (No. 133759), allotype (No. 133760) and five paratypic Form I males (No. 133761) are deposited in the National Museum of Natural History (Smithsonian Institution). Four paratypic Form I males, three juvenile males and two juvenile females have been retained in the private collection of the senior author These individuals were collected with the type-series on September 14, 1971. The juveniles collected in July of 1969 could not be found at the time of this writing.

Remarks.—The three specimens (2 Form I males, one female) mentioned by Jester (1967, p. 518) as having been collected from Conchas Lake on January 15, 1960 are housed in the Smithsonian Institution (No. 118186) as paratypes of *Orconectes causeyi* Jester, 1967. They were listed erroneously as the first observation of *Orconectes causeyi* and were designated as part of the paratypic-

series (p. 521). They are here included in the type-series of *Orconectes deanae.*

When Jester first collected crawfishes from Lake Conchas, he sent the three specimens mentioned above to Dr. Horton H. Hobbs, Jr., for examination, and, believing them to be conspecific with other specimens we had taken from the Lake, donated them to Dr. Hobbs. Unfortunately, not until after Jester's description of *O. causeyi* had been published was it discovered that two species were represented in the type-series, the three specimens first collected differing from all of the others. The difference of opinion between Hobbs and Reimer concerning the relationships of *O. causeyi* as recorded by Jester (p. 523) is understandable. The specimens examined by them belonged to different species.

Associates.—Only one other crawfish has been taken from the lake, *Orconectes causeyi* Jester. *Orconectes causeyi* was collected from the same shoreline area that yielded *Orconectes deanae* and often from under the same rock.

Relationships.—*Orconectes deanae* belongs to the Palmeri Group of the Virilis Section as evidenced by the obliterated areola, configuration of the chela, shape of the antennal scale, and construction of the gonopod and annulus ventralis. Its closest affinities seem to be with *Orconectes palmeri longimanus* (Faxon, 1898) which also occurs in the Canadian River of Oklahoma. It can easily be distinguished from this species by differences in the curvature of the terminal elements of the gonopods. In *O. p. longimanus* they are only gently curved, never to the degree found in *O. deanae.*

Orconectes causeyi is a member of the Virilis Group of the Virilis Section but is not closely related to the new species, although it apparently is native to the upper Arkansas drainage (Dean, 1969, p. 5), including the South Canadian River.

Etymology.—This new species is named in honor of Mrs. Elsie Dean, the junior author's former secretary with the New Mexico Dept. Game and Fish, whose capacity for high quality work is exceeded only by her concern for the success and happiness of her co-workers. This species is named for Elsie as a small token of great esteem.

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PROCAMBARUS (GIRARDIELLA) CURDI, A NEW CRAWFISH FROM ARKANSAS, OKLAHOMA, AND TEXAS (DECAPODA, ASTACIDAE)[1]

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ABSTRACT

Procambarus (Girardiella) ***curdi*** is described from material collected in the Red River drainage of Arkansas and Oklahoma and the Brazos River drainage of Texas. Its closest affinities are with *Procambarus simulans simulans* (Faxon) which occurs in the same drainage systems.

While working on the crawfishes of Arkansas in 1961–1963 (Reimer, 1964), some crawfishes were collected among which were individuals similar to, yet quite distinct from *Procambarus simulans simulans* (Faxon, 1884). At the time, only a limited area of the range of *Procambarus s. simulans* was examined. When a thorough study of the subgenus *Girardiella* was undertaken (Reimer, 1969a) these individuals were recognized as representing a distinct species with an interesting distribution in Arkansas, Oklahoma, and Texas. *Procambarus curdi* represents the sixth taxon to be assigned to the subgenus *Girardiella*.

Procambarus (Girardiella) ***curdi***
new species
(Figures 1–9)

Cambarus simulans.—Creaser and Ortenburger 1933:42, Fig. 18 (in part).

Procambarus simulans simulans.—Reimer 1964:28 (in part), 1969b:56 (in part).

Procambarus A Reimer and Clark, Southwestern Naturalist (in press).

Diagnosis. Rostrum without lateral spines, acumen reduced; areola narrow with two rows of punctations at narrowest part; postorbital ridges terminating cephalically without spine; cervical spine absent or reduced to small tubercle; brachiostegal spine reduced; suborbital angle reduced; antennal scale widest at mid-length; palm of chela without beard. First pleopod of Form I male reaching coxopodite of third pereiopod and terminating in four distinct parts: mesial process noncorneous, subspiculiform, extending beyond other terminal elements; cephalic process noncorneous, small; caudal process, truncate; lamellated part of caudal process corneous flattened lateromesially, narrow, distal margin rounded; central projection corneous, large, subtriangular, flattened lateromesially, slightly longer than caudal process. Cephalic shoulder rounded. Annulus ventralis subovate; cephalic half with broad V-shaped trough, bordered laterally by tuberculate prominences; sinus originating at mid-ventral line, running sinistrad, forming sharp arc on sinistral half, running dextrad to midline, bending caudally, terminating before reaching caudal margin.

Holotypic Male, Form I. Body ovate. Abdomen narrower, longer (14.9, 34.5 mm) than thorax (19.9, 14.1 mm). Cephalic section of telson with four spines in each caudolateral corner, outer spine longest. Width, depth of carapace subequal in region of caudodorsal margin of cervical groove.

Areola narrow (15.7 times longer than wide) two rows of punctations in narrowest part; sides parallel for short distance. Cephalic section of carapace 1.7 times as long as areola (length of areola 36.8% of entire length of carapace).

Rostrum excavate above, sides slightly convergent, cephalic shoulders broadly rounded, acumen reduced, reaching almost to distal border of penultimate segment of peduncle of antennule.

[1] A contribution of the Department of Wildlife and Fisheries Sciences, Texas, Agricultural Experiment Station, Texas A & M University.

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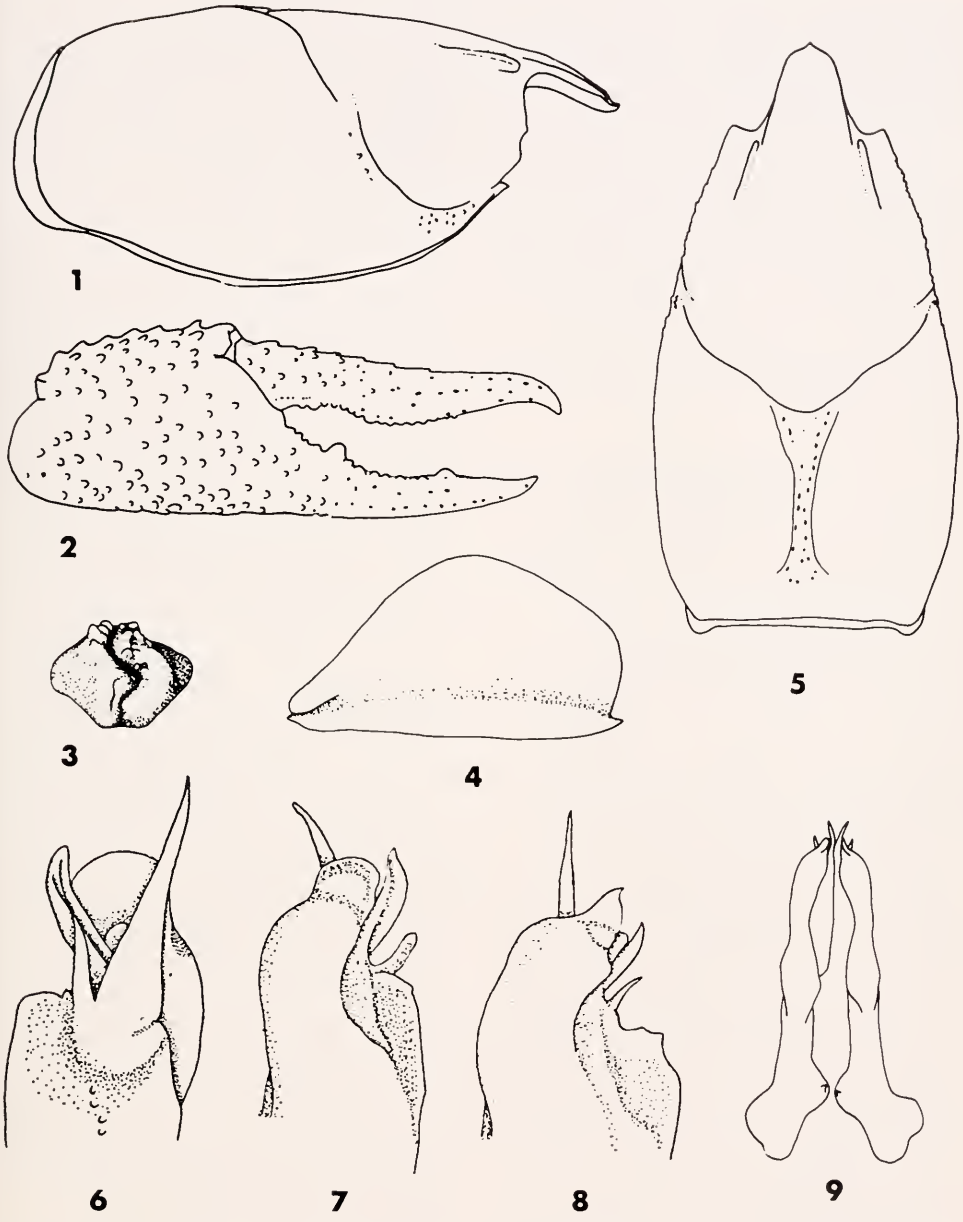

Figures 1–9. Figures 1–7, 9 paratypic *Procambarus curdi* n. sp.: 1, lateral view of cephalothorax; 2, dorsal view of right chela; 3, annulus ventralis of female; 4, antennal scale; 5, dorsal view of cephalothorax; 6, mesial view of terminal elements of first pleopod of Form I male; 7, lateral view of terminal elements of first pleopod of Form I male; 9, ventral view of first pleopods of male. Figure 8, lateral view of terminal elements of first pleopod of Form I male, *P. s. simulaus*.

Postorbital ridges well defined, merging rather abruptly cephalad into carapace, without spine or tubercle. Suborbital angle reduced, rounded; branchiostegal spine slightly reduced. Surface of carapace punctate dorsally, granulate laterally. Epistome broadly subovate; lateral borders raised; cephalic margin with three emarginations.

Antennule of usual form; spine present on ventromesial side of basal segment. Antennae reaching fourth abdominal segment. Antennal scale broad, broadest at mid-length; inner margin angular.

Chela subcylindrical, long. Inner surface of palm tuberculate, rest of surface covered with punctations; palm without beard. Fingers slightly gaping. Opposable margin of dactyl with row of 16 (13 on left) rounded tubercles, denticles along distal half; upper surface with row of tubercles along proximal half. Opposable margin of immovable finger with 13 (14 on left) rounded tubercles, minute denticles scattered along entire length.

Carpus of first pereiopod longer than wide (11.7–8.0 mm); subequal in length to that of inner margin of palm of chela (11.1 mm); shallow, longitudinal groove above; dorsomesial and mesial surfaces tuberculate, otherwise sparsely punctate. Six larger tubercles along distomesial margin, few reduced tubercles along mesial surface.

Merus of first pereiopod slightly punctate mesially and laterally; few tubercles scattered along dorsal surface, more numerous distally; lower surface with two rows of tubercles, outer row of 10 smaller than inner row of 17, most spike-like; two spines along distoventral border; few reduced tubercles on ventral surface between margins.

Hooks present on ischiopodites of third pereiopods. First pleopod reaching base of third pereiopod when abdomen flexed; terminal portion of appendage without setae on cephalic surface. Appendage ending in four distinct parts. Mesial process subspiculiform, noncorneous, extending beyond other terminal elements, bent slightly laterally. Cephalic process small, noncorneous, arising from mesial surface, directed slightly cephalically. Caudal process truncate, corneous, making up caudolateral portion of tip; lamellated part of caudal process flattened lateromesially, narrow, distal margin rounded, slightly cupped, cup opening laterally; adventitious process absent; caudal hump prominent. Central projection large, corneous, subtriangular, flattened lateromesially, slightly longer than caudal process, bent slightly laterally. Cephalodistal shoulder rounded.

Allotypic female. The annulus ventralis is subovate. A broad V-shaped trough extends down the cephalic half bordered by tuberculate elevations laterally. The sinus originates cephalically on the median line and extends sinistrally before forming a sharp arc on the sinistral half. It then runs to the mid-line, before bending caudally. It terminates just before reaching the caudal margin.

Measurements (in millimeters). Male (Form I) Holotype: Carapace, height 18.1, width 19.9, length 38.3; areola, width 0.9, length 14.1; rostrum, width 5.4, length 7.2; abdomen, width 14.9, length 34.5; right chela length of inner margin of palm 11.1, width of palm 12.7, length of outer margin of hand 33.5, length of movable finger 21.5. Female Allotype: carapace, height 16.3, width 17.1, length 32.9; areola, width 0.8, length 11.8; rostrum, width 4.3, length 6.9; abdomen, width 13.7, length 32.9; chelae missing.

Type locality. Navasota River, NE of Bryan on U.S. Highway 190, Brazos County, Texas. The holotype and allotype were collected by the author on 2 June 1968.

The types were collected from burrows on the west bank of the River below the bridge. Recent rains had formed shallow pools some distance from the main river basin, which was overflowing. The crawfish were from around these pools. The burrows had only one opening and descended at an angle to an unknown depth. The crawfish were all taken at a depth of about two feet. Some of the burrows were capped with chimneys up to five inches in height.

Approximately four or five feet to the east of where *Procambarus curdi* was taken, there was a very heavy growth of grass, and immature *Fallicambarus hedgpethi* (Hobbs, 1948) were taken from small pot holes made by car and tractor wheels. No burrows were observed in this area, however, and *F. hedgpethi* was not collected from around or in the pools under the bridge.

Disposition of types. The holotypic male and allotypic female (Nos. 144350 and 144351, respectively) are deposited in the National Museum of Natural History (Smithsonian Institution). All paratypes have been placed in the author's private collection.

Relationships. In 1972, Hobbs reviewed the genus *Procambarus* and erected subgenera for various Groups and Sections within the

genus. The members of the Section Gracilis Ortmann, 1905, which includes *Procambarus s. simulans*; *Procambarus s. regiomontanus* Villalobos, 1954; *Procambarus tulanei* Penn, 1953; *Procambarus gracilis* (Bundy, 1876); and *Procambarus hagenianus* (Faxon, 1884), were placed in the subgenus *Girardiella*, proposed by Lyle in 1938. *Procambarus curdi* seems to have its closest affinities with *P. s. simulans*, *P. s. regiomontanus* and *P. tulanei*, sharing with them the same body conformity but differing in the shape of the rostrum, antennal scale and gonopod. The width-length ratio of the antennal scale as well as the rostrum is less in *P. curdi* than in the above species and the distal spine of the antennal scale and rostrum (acumen) is usually more reduced. The lamellated part of the caudal process is flattened laterome-sially in *P. curdi* rather than cephalocaudally as in *P. s. simulans*. The caudal process is strongly bent caudally in *P. curdi* (as in *P. s. simulans*) rather than straight or only slightly bent as in *P. tulanei* and *P. s. regiomontanus*.

Within the subgenus *Girardiella*, *P. gracilis* and *P. hagenianus* seem to be only distantly related to *P. curdi*. The body, rostrum and antennal scale are more reduced and the cephalothorax is neither spiny nor tuberculate as it is in *P. curdi*. Too, the chelipeds of *P. gracilis* and *P. hagenianus* are shorter, broader and more compressed than in *P. curdi*. The position of the terminal elements of the gonopod of *P. hagenianus* resembles somewhat the condition found in *P. curdi* in that the lamellated part of the caudal process is flattened laterome-sially in both. However, the cephalic process is absent in *P. hagenianus* and the differences in the general body form of the two shows that the cephalic process is not an indication of a close relationship. The terminal elements of *P. gracilis* are more reduced than in *P. curdi*.

The areola, being narrow in *P. curdi*, can be used to distinguish it from *P. gracilis* and *P. hagenianus* which have a closed areola and *P. tulanei* with a wide areola.

Specimens examined. ARKANSAS: *Little River County*—12.5 mi. W. of Ashdown. OKLAHOMA: *Bryan County*—Durant Fish Hatchery at Armstrong. *Choctaw County*—0.4 mi. W. of Swink on U.S. Hy. 70. *Kiowa County*. *McCurtain County*—Small Drain N of Idabel High School; Airport pond NE of Idabel; 0.5 mi. S, 0.25 mi. W of Idabel; Railroad pond S of Idabel. TEXAS: *Brazos County*—Navasota River basin; small drainage creek, SE city limits of Bryan at St. Hy. 6. *Grimes County*—Thomas Cr. S of Anderson.

The collection from Kiowa County, Oklahoma was first reported by Creaser and Ortenburger in 1933. The only label with the collection reads "Kiowa County," and the exact locality for this collection cannot be determined.

Etymology. This species is named in honor of Milton Curd of Oklahoma State University, Stillwater, Oklahoma.

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TULANE STUDIES IN ZOOLOGY AND BOTANY

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PHYTOGEOGRAPHIC AND ECOLOGIC RELATIONSHIPS OF THE FLORA OF BRETON ISLAND, LOUISIANA

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Abstract

The flora of Breton Island, Plaquemines Parish, southeastern Louisiana, 3 miles long by about ½ mile wide, was studied intermittently between 1958 and 1962, the year the island was bisected by a hurricane. The composition of the flora was compared with records published sixty years previously. This salt-spray plant community was composed of 84 species of vascular plants and 3 mosses. Six land forms and their characteristic plant associations were recognized and changes effected during the four year period were noted. The disappearance of ten species abundant sixty years before may be attributed to the effect of salt spray and occasional hurricanes. From the phytogeographic standpoint most species were found to be members of temperate rather than tropical floras, probably due to the severity of the climate militating against the persistence of tropical species. Dispersal agencies are discussed.

Introduction

Visits to Breton Island offered an unusual opportunity to compare the flora of 1958–1962 with that of sixty years earlier when Lloyd and Tracy (1901) collected plants on Breton and other islands of the Gulf of Mexico. The paucity of publications on Louisiana offshore islands, in a region which the oil industry is rapidly exploiting, accentuates interest in this area.

Breton Island is located about 35 miles northeast of the Mississippi River at 29°28° North Latitude. Its central location along the northern border of the Gulf of Mexico makes it both receptive to species capable of migrating from Caribbean sources, and receptive to species arriving by wind, birds, or rafting from the continental coastal plain which extends from Texas to New England. In 1962 the island was divided into two islets, North and South Breton, by a channel about 400 yards wide. The subject of this paper, what is now "South Breton," was formerly three miles long by about one-half mile at its greatest width. It is the most southerly member of a crescent shaped chain of islands known as the Chandeleurs. Judging from maps of the early 18th century, we suspect that Breton Island was not considered geographically one of the Chandeleurs simply because it was probably charted later than the islands to the northeast. At least by 1718, and probably earlier, explorers sailed within a mile or two of Breton (Paullin, 1932).

The substrate of the islands consists almost entirely of broken shells of *Pecten* and *Venus* carried from the adjacent bottoms by offshore wave action (similar to that along the north shore of Yucatan, though in the Chandeleurs there is no longshore drift from a land connection) (Galtsoff, 1954). Year by year Breton Island has been eroding along its eastern and southern shore. Wind and

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wave action had reduced its size from eleven to five miles in length since Lockett's description in 1870 (Russell, 1936). The ultimate fate of the island may be complete inundation as was the case of nearby Battledore Island, the flora of which had been studied by Lloyd and Tracy (1901).

The gulf insular flora of Louisiana was floristically first described by Lloyd and Tracy (1901), Grand Isle later by Brown (1930), the delta vegetation by Penfound and Hathaway (1938) and the Chandeleur flora by Lemaire (1961). Oosting (1954) reviewed the fundamental literature on maritime strand vegetation of the southeastern United States. He pointed out that climax, in its various aspects, is the chief concern of textbooks of plant ecology. He then brought together from the literature what is known of community dynamics and related ecologic processes and conditions on the sand strand, so that they may be correlated more effectively with textbook generalizations. Lloyd and Tracy's collections on Breton Island in 1900 present an opportunity to compare the past flora with that encountered sixty years later and to suggest the dynamism of plant associations. The marine flora of the area has been discussed by Humm and Caylor (1957).

Severe but erratic climatic conditions are characteristic of Breton Island, as apparently of all Gulf and Atlantic strand environments (Oosting, *op. cit.*). The summers are intolerably hot and the winters often penetratingly cold, wet, and windy. The topography of Breton Island Island is one of continual change. From one visit to the next, shores once dotted with ponds and cut with lagoons are covered over by driving drifts of sand. The north and west ends of the island are particularly vulnerable to wind and wave action, while the entire leeward side, dominated by Black or Honey mangrove (*Avicennia nitida*), is relatively stable. (Nomenclature of this species accords with E. L. Little, *Phytologia* 8:49–57. 1961.) According to Davis (1940, 329–331, pl. 5, fig. 1, and pl. 11, fig. 1) the leeward side was certainly increasing by the continuous reproduction of Black mangrove when he studied the habitat.

Animal life on the island was varied and particularly rich in numbers and species of transient birds. Native rice rats, *Oryzomys palustris* (Harlan), swamp rabbits, *Sylvilagus aquaticus* Bachman, and introduced coypu or nutria, *Myocaster coypus* E. Geoffroy St. Hilaire were the most common mammals. We observed the following birds at their nests: snowy egrets, *Leucophoyx thula* (Molina) and Louisiana herons, *Hydranassa* tricolor (Müller) in the bayberry shrubs, willets, *Catotrophorus semipalmatus* (Gmelin) in the sedge association, clapper rails, *Rallus longirostris* Boddaert on the tops of the primary dunes, black skimmers, *Rynchops nigra* L. and common nighthawks, *Chordeiles minor* (Forster) on the sand flats, boat-tailed grackles, *Cassidix mexicanus* (Gmelin) in the black mangroves and red-winged blackbirds, *Agelaius phoeniceus* (L.) in the grasses bordering the mangrove (Negus, Gould and Chipman, 1961).

Acknowledgments

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Survey and Collection of the Flora

We traveled to the island several times by sea plane, landed at an islet called "North" Breton, and then motored by 15 foot skiff to "South" Breton or Breton Island proper. A few trips were made entirely by boat. With the skiff we explored the network of waterways among the Black mangroves in the lee of the island. We collected on foot along its length (windward side) and interiorly wherever the Wax myrtle was penetrable.

Donald E. Stone, then a member of the faculty of Tulane University, collected on Breton Island on 29 July 1958, his collection numbers prefixed by "S" (as "S-257") and Ewan (E-) on 4 April 1960. Gould (G-) collected on the following dates: 18 June 1959, 26 March 1959, 4 April 1960, and 13 January 1962. Lemaire's (L-)

collections, to which we make frequent references, were taken 27, 29, 30 October 1959; 15 June, 31 August, and 1 September 1960. Our collections, those of Stone, and a prime set of Lemaire's are deposited in the Tulane University Herbarium.

Survey of Species Present

The following list of 84 species of vascular plants and three mosses were collected or observed on Breton Island between July, 1958 and January, 1962. The arrangement and nomenclature follows chiefly Small (1933); the grasses, Hitchcock (1950). Monographic studies consulted are noted under remarks. The entry "Lemaire (1961)" under remarks, when no other collector or number is indicated, denotes that Lemaire collected or observed the species but we did not.

List of Plants

Genus and Species	Collections	Remarks
Mosses		
Bryum bicolor Dicks.	G-107	det. W. D. Reese
Bryum capillare Hedw.	G-106	det. W. D. Reese
Physcomitrium pyriforme Brid.	G-106	det. W. D. Reese
Cymodoceaceae		
Cymodocea manatorum Aschers.		Lemaire, 1961
Halodule wrightii Aschers.		Lemaire, 1961
Hydrocharitaceae		
Thalassia testudinum Koenig & Sims		Lemaire, 1961
Gramineae		
Andropogon glomeratus (Walt.) B.S.P.		Lemaire, 1961
Chloris petraea Swartz		Lemaire, 1961
Distichlis spicata (L.) Greene		Lemaire, 1961
Eragrostis elliottii S. Wats.	L-1691, 1712	
Eragrostis oxylepis (Torr.) Torr.	L-808, 1732	
Panicum amarulum Hitchc. & Chase		Lemaire, 1961
Panicum portoricense Desv.	L-1720	
Panicum repens L.	S-267	Lemaire, 1961
Paspalum ciliatifolium Michx.		Lemaire, 1961
Setaria geniculata (Lam.) Beauv.	L-1682	
Spartina alterniflora Loisel		Lemaire, 1961
Spartina patens (Ait.) Muhl.	G-53, 21, 58, 72; S-270, 280	Lemaire, 1961, det. J. Swallen
Spartina spartinae (Trin.) Merr.		Lemaire, 1961
Sporobolus virginicus (L.) Kunth	L-803, 636; G-56	
Triplasis purpurea (Walt.) Chapm.	L-807	
Uniola paniculata L.	G-81, 83, 84	
Cyperaceae		
Cyperus filicinus Vahl	G-47, 60; S-258	det. R. K. Godfrey
Cyperus lecontei Torr.		Lemaire, 1961
Cyperus polystachyos Rottb.		Lemaire, 1961
Cyperus retrorsus Chapm.	S-256	det. R. K. Godfrey
Eleocharis albida Torr.	L-634	det. R. Kral
Eleocharis geniculata (L.) R. & S.	G-109	det. R. Kral
Fimbristylis castanea (Michx.) Vahl	L-1687; G-25, 30, 32, 70, 74; S-250, 259, 268	det. R. Kral; Lemaire, 1961

Commelinaceae		
Commelina erecta var. *angustifolia* (Michx.) Fern.		Lemaire, 1961
Juncaceae		
Juncus megacephalus M. A. Curtis	S-257; L-637	
Juncus roemerianus Scheele		Lemaire, 1961
Liliaceae		
Smilax auriculata Walt.	G-112	
Yucca gloriosa L.	E-19888	
Myricaceae		
Myrica cerifera L.	G-5; S-282; E-19880, 19881, 19886	
Urticaceae		
Parietaria floridana Nutt.		Lemaire, 1961
Polygonaceae		
Rumex persicarioides L.	S-274	
Chenopodiaceae		
Salicornia virginica L.	E-19889; G-37; S-276	
Phytolaccaceae		
Phytolacca americana L.		Lemaire, 1961
Batidaceae		
Batis maritima L.	G-20, 75; S-277; E-19890	
Cruciferae		
Cakile edentula (Bigel.) Hook.	G-2, 3, 16, 100; S-261	
Lepidium virginicum L.	G-45, 71, 104, 112; S-252, 278, 279; E-19877	cf. Hitchcock, 1936
Rosaceae		
Rubus trivialis Michx.	G-6, 102; E-19876	Lemaire, 1961
Leguminosae		
Daubentonia drummondii Rydb.	G-76; S-283; L-1701	
Strophostyles helvola (L.) Ell.		
Euphorbiaceae		
Chamaesyce ammanioides (H.B.K.) Small	L-1693	det. J. Ewan
Chamaesyce ingallsii Small	L-1692	Lemaire, 1961
Chamaesyce polygonifolia (L.) Small	L-1708	det. J. Ewan
Chamaesyce supina (Raf.) Moldenke	L-1694	
Croton punctatus Jacq.	G-26, 59, 91; S-264; E-19883	det. M. C. Johnston
Malvaceae		
Hibiscus lasiocarpus Dav.		Lemaire, 1961
Kosteletzskya virginica var. *altheaefolia* Chapm.	L-1685	
Cactaceae		
Opuntia stricta Haw.	E-*S.n.*; G-6, 115	det. L. Benson
Onagraceae		
Oenothera humifusa Nutt.	G-108, 103, 110; S-255, 262; L-959; E-19884	

Umbelliferae		
Hydrocotyle bonariensis Lam.	E-19887; G-35; S-265, 253	Lemaire, 1961
Ptilimnium capillaceum (Michx.) Raf.	G-52, 46; S-263, 251	
Plumbaginaceae		
Limonium carolinianum (Walt.) Britt.	G-66	det. J. L. Luteyn
Limonium carolinianum var. *augustatum* Blake	G-112	det. J. L. Luteyn
Limonium nashii Small	L-355	det. J. L. Luteyn
Gentianaceae		
Sabatia arenicola Greenm.	S-254; L-641, 1017; G-50	cf. Wilbur, 1955
Sabatia stellaris Pursh	E-17896; G-39, 55	cf. Wilbur, 1955
Asclepiadaceae		
Cynanchum palustre (Pursh) Hel.	L-1684	
Convolvulaceae		
Ipomoea pes-caprae (L.) Sweet		Lemaire, 1961
Ipomoea stolonifera (Cyrill.) Poir.	G-27	Lemaire, 1961
Boraginaceae		
Heliotropium curassavicum L.	L-640; G-33; S-275	
Verbenaceae		
Lippia nodiflora (L.) Michx.	E-19885	
Avicenniaceae		
Avicennia nitida Jacq.	G-14; S-273; E-19891	
Labiatae		
Teucrium canadense L.	G-43	cf. McClintock & Epling, 1946
Scrophulariaceae		
Agalinis maritima var. *grandiflora* (Benth.) Pennell	G-18; L-635, 798	
Bacopa monnieri (L.) Pennell	G-13, 38; S-266	cf. Pennell, 1935
Linaria canadensis var. *texana* (Scheele) Pennell	G-113; L-962	
Cucurbitaceae		
Melothria pendula L.	L-1703	
Compositae		
Anthemis cotula L.		Lemaire, 1961
Aster tenuifolius L.	L-1709	
Baccharis halimifolia L.	G-4; L-354; S-271, 281; E-19882	
Borrichia frutescens (L.) DC.	G-17, 111; S-269, 271a; 271b	
Conyza canadensis (L.) Cronq.	L-1700	
Eclipta alba (L.) Hassk.	L-1702	
Erechtites hieracifolia (L.) Raf.	G-86, 85, 105; L-1704	
Eupatorium serotinum Michx.	E-19879	
Iva frutescens L.		Lemaire, 1961
Mikania scandens (L.) Willd.	E-19892; L-1714	
Pluchea camphorata (L.) DC.	L-1706	
Pluchea foetida (L.) DC.	L-1707	
Pluchea purpurascens (Sw.) DC.	L-1705	

Analysis of Vegetation

The methods employed in describing the vegetation of Breton Island are based on the general premise that the entire flora is a salt spray community (cf. Wells, 1939) and that the various associations of plants are primarily due to varying salt tolerance of different species. Correlation of tolerance to salt by individual plants and their subsequent zonation with the intensity of air borne spray is well substantiated (cf. reviews by Oosting, 1954 and Boyce, 1954).

The intimate relationship of species composition is best treated in conjunction with the land form of a strand flora. Our topographic classification is adapted from Martin (1959).

The six zones of vegetation were distinguished from a mere scattering of beach plants dominated by *Cakile* to the dense bay shore tangle of Black mangrove. Species in each association are listed and the abundance of each with regard to its particular association:

*	rare
**	infrequent
***	frequent (indicating scattered presence)
****	common (indicating presence over most of the island)
*****	abundant

Six land forms were characterized by specific plant associations.

1. The outer beach was most vulnerable to very high tides; of all the terrains it supported the least vegetation.

Cakile association

Batis maritima	***
Cakile edentula	****
Heliotropium curassavicum	**
Hydrocotyle bonariensis	***

2. The inner beach has been inundated annually during hurricanes or high winds. On the eastern half of the island where there is full exposure to the prevailing southeast wind, no inner beach exists. (Fig. 1)

Sedge association

Baccharis halimifolia	***
Bacopa monnieri	**
Borrichia frutescens	***
Croton punctatus	***
Cyperus filicinus	***
Distichlis spicata	***
Eleocharis geniculata	***
Fimbristylis castanea	*****
Heliotropium curassavicum	**
Hydrocotyle bonariensis	****
Juncus megacephalus	**
Lepidium virginicum	***
Limonium carolinianum	*
Linaria canadensis	**
Myrica cerifera	***
Oenothera humifusa	***
Ptilimnium capillaceum	***
Rumex persicarioides	*
Sabatia arenicola	***
Sabatia stellaris	****
Spartina patens	*****
Uniola paniculata	**

3. Foredune. The primary dune is highest along the eastern half of the island and becomes gradually lower toward the west end until it is absent. The outer beach comes progressively closer to the primary dune (Fig. 1) toward the narrow strip at the north end where the *Myrica* covered dune yields to constant wave action.

Croton association

Croton punctatus	*****
Hydrocotyle bonariensis	**
Ipomoea angustifolia	***
Lepidium virginicum	***

4. Backdune.

Wax myrtle association

Baccharis halimifolia	****
Myrica cerifera	*****
Opuntia stricta	***
Teucrium canadense	**

5. A secondary dune exists as a high land formation on the eastern half of the island. It covers about three acres. The presence of very old and large storm-washed boles suggests that severe hurricanes have repeatedly inundated the island.

Opuntia-Yucca association

Bryum bicolor	*
Bryum capillare	*
Erechtites hieracifolia	**
Opuntia stricta	*****
Physocomitrium pyriforme	*

Figure 1. Vegetation of outer beach, eastern half of Breton Island, January, 1962. *Myrica*, on left, appearing dark; *Croton*, clothing the primary dune, gray and withered appearance due to recent freeze; *Opuntia*, foreground, being covered by drift. No inner beach present.

Rubus trivialis	***
Smilax auriculata	*
Yucca gloriosa	****

6. The leeside shore. The only terrain where the overlay of the substrate is not composed entirely of sand. The death and decay of Black mangrove has contributed to the accumulation of soft black muck.

Black mangrove association

Avicennia nitida	*****
Batis maritima	****
Borrichia frutescens	***
Salicornia virginica	****

Discussion

The report of Lloyd and Tracy (1901) provides data for the comparison of floras after an interval of sixty years. The following species were abundant in 1900 and still held their dominance with two exceptions:

Avicennia nitida
Batis maritima
Borrichia frutescens
Fimbristylis castanea
Mikania scandens (rare in 1958–62)
Myrica cerifera
Opuntia
Sabatia stellaris
Salicornia sp.
Uniola paniculata
(infrequent in 1958–62)
Yucca gloriosa

The following species were rare or absent in 1900 and were common, 1958–1962.

Croton punctatus
Daubentonia drummondii
Hydrocotyle bonariensis

The following species (in the nomenclature of Lloyd and Tracy) were abundant in 1900 but were absent, 1958–62.

Asclepias amplexicaulis Michx.
Bradburya virginiana (L.) Kuntze
Cathartolinum floridanum (Planch.) Small
Chaetochloa magna (Griseb.) Scribn.
Cassia (*Chamaecrista*) sp.

Figure 2. Clearing within *Myrica* stand, same location as Figure 1, *Opuntia* colony flanked by *Croton*. Some *Opuntia* clumps four meters across and nearly 2 meters high.

Dondia linearis (Ell.) Heller
Gnaphalium purpureum L.
Ilex vomitoria Ait.
Iva imbricata Walt.
Physalis angustifolia Walt.

The disappearance of the last three species listed is not easily explained. The sedge association and to a lesser extent the *Croton* association are the most unstable zones on the island. All of the species of the inner beach and primary dune (now common; now absent) are characteristic of these two associations. Vulnerability to salt spray is the obvious explanation for this instability. Several other changes in the Breton Island flora may be noticed by a comparison of our observations with those made by Lloyd and Tracy in 1900. Lloyd and Tracy pointed out that the dominance of *Panicum amarulum* on the upper beaches of the Gulf islands (including Breton) was comparable to the dominance of the "sand-binding grass" *Uniola paniculata* on the Florida dunes (Webber, 1898) and on the Ocracoke Island, North Carolina strand (Kearney, 1900). On Breton Island, *Panicum amarulum* was now replaced by *Fimbristylis castanea* and *Spartina patens*. *Uniola paniculata* remained only as a small colony, less than a half acre, in a blow-out of the primary dune at the approximate center of the island. In 1900 it was abundant, but on our visits was now infrequent. This is noteworthy because Wells (1939) rates *Uniola paniculata* as even more salt spray tolerant than either *Myrica cerifera* or *Ilex vomitoria*. The decline here is probably due to the growth of the dune and the consequent cutting off of some of the salt spray.

In 1900, *Ipomoea pes-caprae* and *I. stolonifera* formed a "network covering the soil" on the upper beach of Breton Island. Lloyd and Tracy noted that usually these two species were scarce on the Gulf islands, but that Breton was an exception. They attribute the *usual* condition to the "pre-eminently tropical" ecological requirements of these species. Sixty years later *Ipomoea pes-caprae* was rare on Breton Island but *I. stolonifera* was frequent.

Throughout the period of our study the

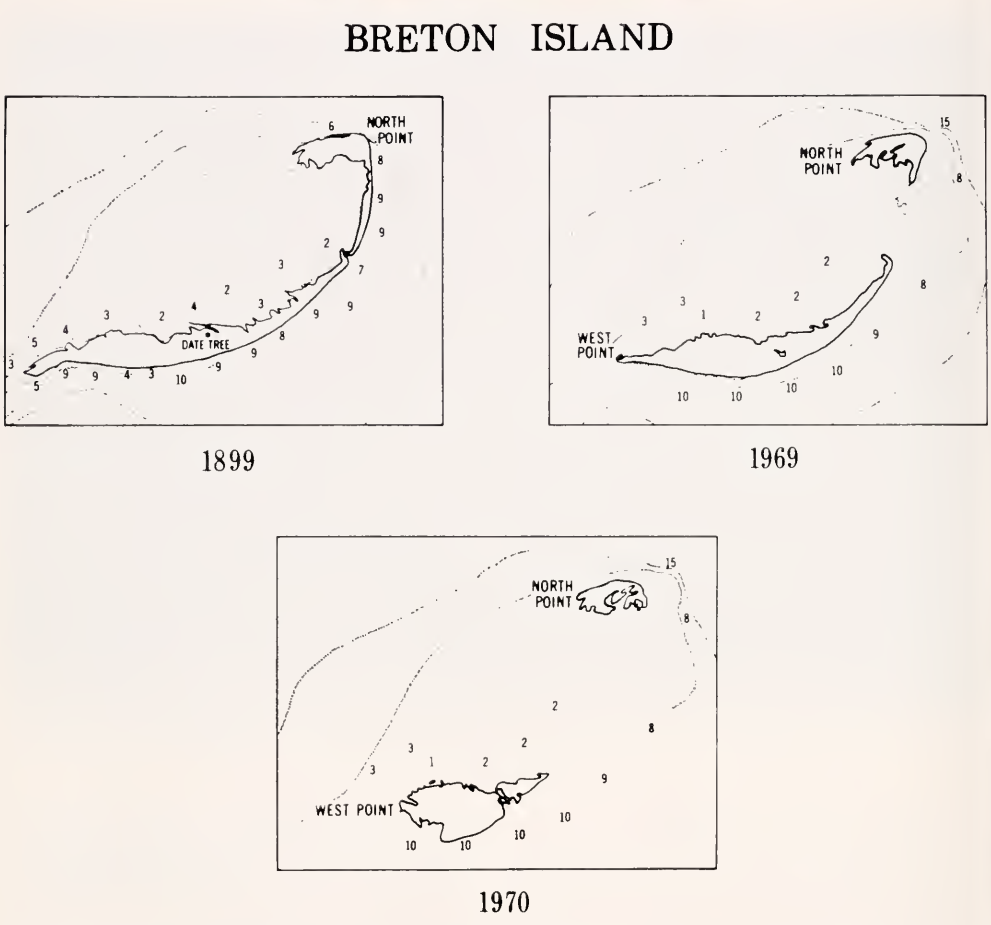

Figure 3. The gradual disappearance of Breton Island as shown by comparison of extracts from United States Coast and Geodetic Survey charts. Fine dotted lines indicate sand shoals probably a part of a much larger land mass in the distant past.

so-called "low stature dunes" of the upper beach (Lloyd and Tracy, 1900) were covered with *Croton punctatus* and *Myrica cerifera*. In 1900 these dunes were "clothed with a thicket of *Ilex vomitoria* and *Myrica gale* [*cerifera*]."

Lemaire's collections further document the changing nature of the Breton flora since 1900 and the seasonal differences it displays. Lemaire collected or observed 47 species of plants which we failed to record; he did not record seven we found. He scored 25 as rare or infrequent, ten as infrequent and five as common. Lemaire collected during late summer and fall; our collections, in the spring and early summer. That most of his 47 species were transitory and not due to differences in collecting experience is partially supported by Boyce (1954). During three summers on Cape Fear, North Carolina, Boyce noted fourteen transitory species which do not ordinarily reproduce in the salt spray community. Five genera are the same as those collected by Lemaire (in three cases* the species are identical): *Conyza canadensis**; *Phytolacca americana**; *Andropogon glomeratus**; *Aster walteri*; and *Sporobolus poiretii*.

During the span of four and a half years over which we visited Breton Island, several changes occurred in the apparent abundance of two common species. For approximately two years, 1958 to 1960, *Daubentonia* shrubs, 8 to 10 feet high, were a prominent feature,

and during early summer, a brilliant yellow spectacle, between the upper and lower beach. In 1960, following several hurricanes, they virtually disappeared. In January, 1962, *Daubentonia* were again common, about 50 yards inland from their former location, along the primary dune and among the dense stand of *Myrica*. They were also dispersed among *Baccharis* shrubs on the upper beach in sedge association. *Fimbristylis* and *Spartina* were still abundant.

Opuntia was always present (1958–1962), in abundance on the secondary dune and sparingly present in the lee of the primary dune in the sheltered clearings of *Myrica*. A few plants grew at the west end and along the border of the secondary dune. Some grew alongside of, and even in the brackish water of, the mangrove swamp. In the primary dune sites, from 1958 to 1960, the *Opuntia* clumps were very small, 6 inches to 1 foot, and spread only a few feet. In January, 1962, despite several hurricanes during 1961 and the coldest winter of the century, *Opuntia* had flourished in the clearings among the *Myrica* (Fig. 2) and spread even below the foredune (Fig. 1) and had grown as high as 5 feet tall with a 12 foot spread.

An attempt to equate floral and topographic zonation with the categories used by Vogl (1966, modified from Purer 1942) is only partially adequate because the entire island is obviously vulnerable to massive inundation during hurricanes. The following list may be close equivalents.

Breton Island	*Vogl's Classification*
Outer beach	Middle littoral zone
Inner beach	Upper littoral zone
Foredune	Maritime zone (not inundated)
Secondary dune	Maritime zone (not inundated)
Leeside shore	Maritime zone (not inundated)

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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 19, No. 3 & 4 March 25, 1977 $3.50

LONGITUDINAL DISTRIBUTION OF THE FISHES OF THE BUFFALO RIVER IN NORTHWESTERN ARKANSAS,

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and

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U.S. Fish and Wildlife Service
Division of Ecological Services, Washington, D.C. 20240

ABSTRACT

A survey of the fishes of the Buffalo River in northwestern Arkansas was conducted over a seven year period. The Buffalo is a free-flowing tributary to the cold tailwater section of the White River below Bull Shoals Dam, and is wholly contained in the Ozark Upland province.

Fifty-nine species were recorded for the river based on 135 collections and literature records. Relatively continuous distribution was shown for 38 species. The general pattern of distribution for the river was one of species addition rather than replacement from headwaters to the mouth.

INTRODUCTION

The Buffalo River in northwestern Arkansas is a wild, free-flowing, Ozark Upland stream. The river courses approximately 135 miles from its headwaters in the Boston Mountains to its confluence with the White River, 27 miles below Bull Shoals Dam.

In 1963 the National Park Service recommended that this last unimpounded stream in the Arkansas Ozarks be designated a National River (Smith, 1963). Very different plans by the U.S. Army Corps of Engineers called for the construction of a dam at Gilbert, Searcy County, which would inundate 50 miles of stream (Smith, 1963). Through the efforts of concerned naturalists, dam construction has been averted and the Buffalo River's scenic beauty has been preserved. In 1972 the 92nd Congress approved the establishment of the Buffalo River as a National River, and a temporary office of the National Park Service was established in Harrison, Arkansas to purchase the necessary land (Mr. Joe Clark, pers. comm.).

The present study originally began as a pre-impoundment survey of the fishes of the Buffalo River. The construction of large hydro-electric dams is known to alter the faunal composition not only within reservoirs, but in tailwaters as well (Moffett, 1942; Summers, 1954; and Pfitzer, 1962). Thus such a study seemed timely. Fortunately, this paper will now serve as a record of the species present and their longitudinal distributions within the Buffalo River, a protected river.

EDITORIAL COMMITTEE FOR THIS PAPER:

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METHODS

Sixteen stations were established on the Buffalo River and its tributary streams between the headwaters and the mouth (Fig. 1). These stations were sampled from one to six times during the summers of 1965 and 1966. The lowermost localities (Stations 1 and 2), at the mouth and 2.0 miles above the mouth, were sampled monthly from October, 1965 to October, 1966. Supplemental collections were made by the senior author from the fall of 1968 to the spring of 1972. A total of 135 collections was made during this study. Over 24,000 specimens were collected using a 115 volt, 1,000 watt AC shocker, and a 10 foot, 3/16 inch mesh nylon seine. Localities in the middle and lower sections of the river were often reached by boat, and much of the electro-shocking was done from the boat. The points on the map indicate the sites where collecting began, or where the boat was launched. When possible, we electro-shocked one or two miles up and downstream from the starting point. Station 3 was a general survey site that covered nearly 5 river miles and was reached by motoring upstream from the mouth. Most of the specimens collected were deposited in the Tulane University Fish Collection.

Three additional stations were designated from collections made by other workers. Station 4, Buffalo River at the mouth of Brush Creek, was sampled by Dr. Kirk Strawn and students from the University of Arkansas in the summer of 1963. Dr. Neil Douglas and Mr. Terry Guidroz, Northeast Louisiana State University, made three collections in the winter of 1972 and the spring of 1973 at Station 11, Buffalo River 5.0 miles northeast of Snowball, Searcy County. The extreme headwater site (Station 19) was based on records by Dr. J.D. Black (1940). Literature records and other collections from the Buffalo River housed at Tulane University (TU) and Northeast Louisiana State University (NLU) were used to determine longitudinal distributions for many species (Table 1).

List of localities and approximate river mileages from the mouth:

1. Mouth of Buffalo River to 0.5 mile upstream, Baxter-Marion counties.
2. Buffalo River about river mile 2, Baxter-Marion counties.
3. Buffalo River, general survey area, river mile 3-8, Marion County.
4. Buffalo River, at the mouth of Brush Creek, river mile 14.6, Marion County, (Strawn and party, 1963).
5. Buffalo River, at the mouth of Clabber Creek, river mile 22, Marion County.
6. Buffalo River, at the town of Rush, river mile 24, Marion County.
7. Rush Creek, at the town of Rush, 0.5 mile above its confluence with the Buffalo River, Marion County.
8. Buffalo River, from State Hwy. 14 crossing to State Park, river mile 28-30, Marion County.
9. Bear Creek, at U.S. Hwy. 65 crossing, about 10 miles above its confluence with the Buffalo River (approximately mile 54), Searcy County.
10. Buffalo River, at Gilbert and U.S. Hwy. 65 crossing, river mile 49, Searcy County.
11. Buffalo River, 5.0 miles northwest of Snowball on County Rd. 377, river mile 65, Searcy County, (Douglas and Guidroz collection, 1973).
12. Richland Creek, near Eula on County Rd. 377, about 4 miles above its confluence with the Buffalo River, Searcy County.
13. Buffalo River, 2.0 miles south of Hasty on State Hwy. 74, about river mile 78, Newton County.
14. Little Buffalo River, at Jasper on State Hwy. 74, 5 miles above confluence with Buffalo River, Newton County.
15. Little Buffalo River, near Parthenon on County Rd. 327, 11 miles above its confluence with the Buffalo River, Newton County.
16. Buffalo River, near Pruitt on State Hwy. 7, about river mile 88, Newton County.
17. Buffalo River, 0.5 mile east of Ponca on State Hwy. 74, about river mile 107, Newton County.
18. Unnamed Creek, one mile south of Ponca on State Hwy. 43, about river mile 108, Newton County.
19. Buffalo River, approximately 4 miles southwest of Mossville, about river mile 120, Newton County (Black, 1940).

ACKNOWLEDGEMENTS

We acknowledge our fellow graduate students at the University of Arkansas and R.K. Strawn who assisted us in the

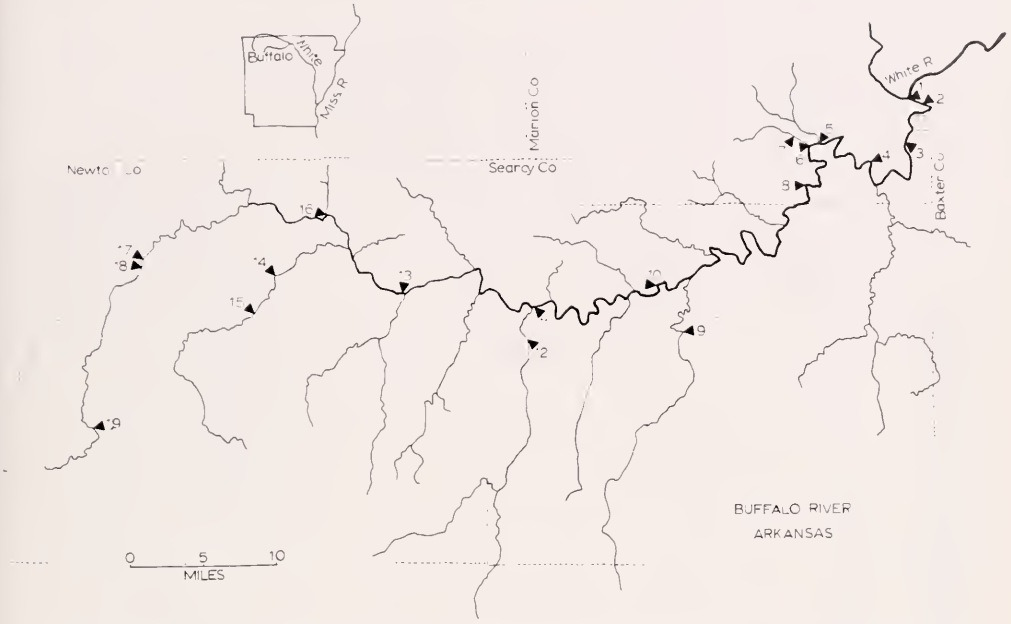


FIGURE 1. Map of the Buffalo River in Northwestern Arkansas, with Collecting Sites.

field during the early part of this study. Special thanks go to Bruce A. Thompson and Julian M. Humphries for aiding the senior author on additional collecting trips from 1968 to 1972.

Thomas M. Buchanan, Neil H. Douglas, and Terry Guidroz kindly provided information concerning collections made in the Buffalo River drainage during 1972 and 1973. Royal D. Suttkus, Tulane University (TU), Neil H. Douglas, Northeast Louisiana University (NLU), and Reeve M. Bailey and Robert R. Miller, University of Michigan Museum of Zoology (UMMZ), kindly allowed us to examine specimens under their care.

R.D. Suttkus and Gerald E. Gunning, Tulane University, and Clark Hubbs, University of Texas, made helpful suggestions regarding the manuscript. The Ozark Society and J.F. Nix gave us permission to use the drainage map adapted from Smith (1963).

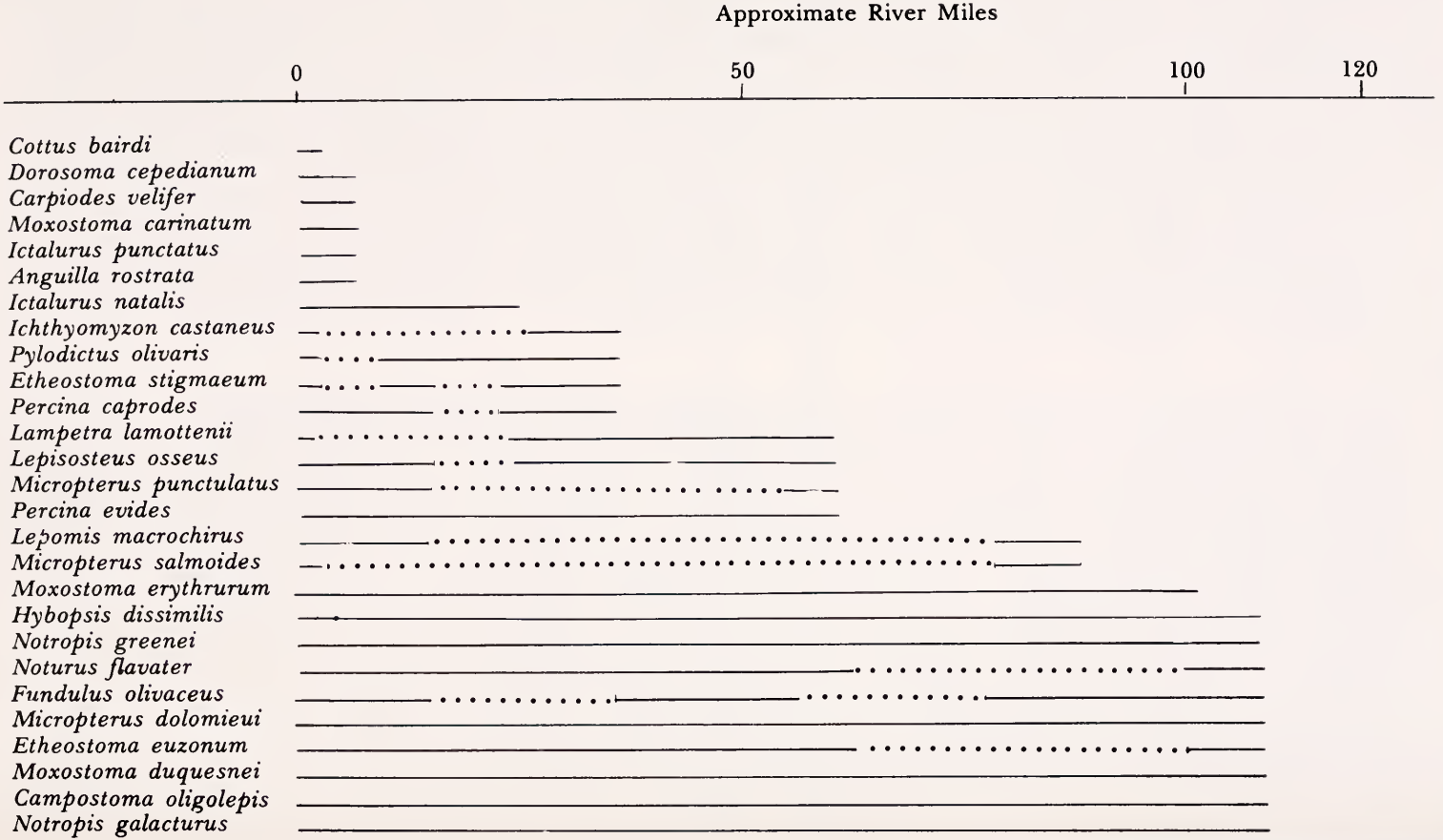
Support for the work done at the University of Arkansas, during 1965 and 1966, was provided by the Office of Water Resources Research, Department of the Interior, through the Arkansas Water Resources Research Center (Grant No. A-001-ARK) as authorized under the Water Resources Research Act of 1964 (PL 88-379). Additional collections were funded, in part, by a Sigma Xi grant to Cashner, 1971, and expenses for museum visits were deferred, in part, by a 1972 Sport Fishing Institute grant to Suttkus.

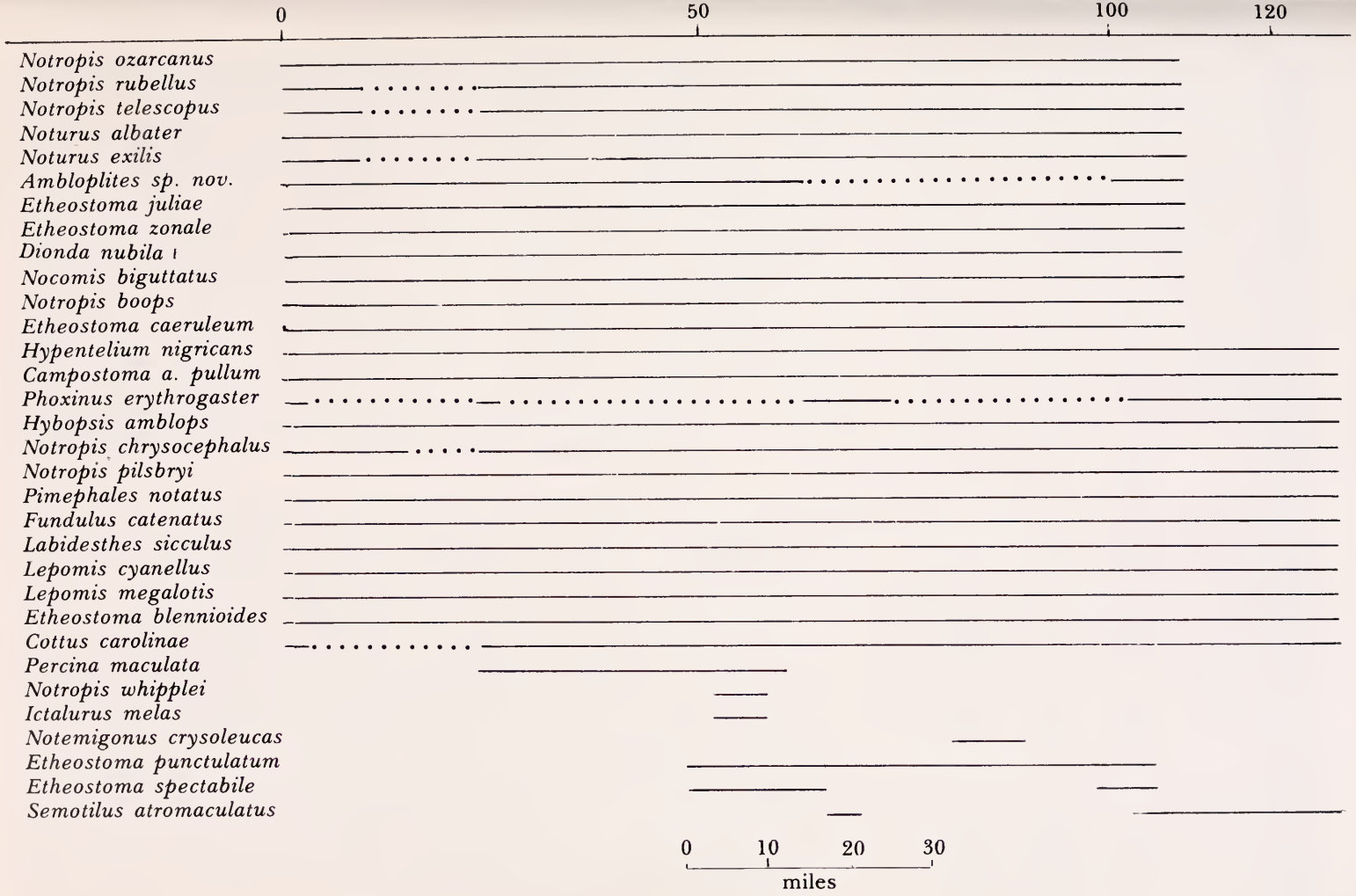
DESCRIPTION OF THE STUDY AREA

The Buffalo River drains an area of 1383 sq. mi. and has an average rate of fall of 5.23 ft/mi (Gladson, 1911). The substrate is primarily gravel and rubble, with some boulders in the headwater section (sites 14-19). In the middle and lower sections, rubble, boulder, and bedrock are the more common bottom types, but there are extensive gravel riffle areas in these regions as well. There is a detectable deposit of silt in the lower reaches where the Buffalo River has its confluence with the White River.

In the summer the flow of the Buffalo River from above Ponca (Site 17) to Gilbert (Site 10) was intermittent. The river in this region consisted of a series of deep pools connected by the very shallow flow of the main channel in the summers

Table 1. Longitudinal distribution of fishes in the Buffalo River, Arkansas. Line is continuous if a species was not missing from two or more successive localities, otherwise the line is dotted.

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Notropis ozarcanus
Notropis rubellus
Notropis telescopus
Noturus albater
Noturus exilis
Ambloplites sp. nov.
Etheostoma juliae
Etheostoma zonale
Dionda nubila
Nocomis biguttatus
Notropis boops
Etheostoma caeruleum
Hypentelium nigricans
Campostoma a. pullum
Phoxinus erythrogaster
Hybopsis amblops
Notropis chrysocephalus
Notropis pilsbryi
Pimephales notatus
Fundulus catenatus
Labidesthes sicculus
Lepomis cyanellus
Lepomis megalotis
Etheostoma blennioides
Cottus carolinae
Percina maculata
Notropis whipplei
Ictalurus melas
Notemigonus crysoleucas
Etheostoma punctulatum
Etheostoma spectabile
Semotilus atromaculatus
0
10
20
30
miles

Table 2. Mean discharge (CFS) for the Buffalo River at two stations during the summers of 1965 and 1966. U.S. Geological Survey (1965 and 1966).

	June		July		August		Calendar Year	
Station	1965	1966	1965	1966	1965	1966	Oct. 1964 to Sept. 1965	Oct. 1965 to Sept. 1966
Buffalo R. at Rush	566	115	305	43.3	66.8	39.8	541	637
Buffalo R. near St. Joe	665	163	375	74.4	99.2	63.8	695	761

of 1965 and 1966.

Farther downstream the flow is more regular. Data gathered by the U.S. Geological Survey during the summer months at Buffalo River stations near St. Joe (Site 10) and Rush (Site 6) are presented in Table 2.

Summer water temperatures in the upper section of the Buffalo River ranged from 25 to 28°C. Downstream water temperatures were higher (28 to 31°C). The Buffalo River is a southwestern tributary of the cold tailwater section of the White River below Bull Shoals Dam. In this section of the White River water temperatures may be as low as 7°C at any time of the year (Brown *et al.*, 1967). During summer months a sharp temperature differential exists between waters of the main channel and the side of the White River receiving the comparatively warm waters of the Buffalo River. This difference in temperature persists over seven miles downstream, where another cold tailwater, the Norfolk River, enters from the north. The water temperatures in the southern side of the White River channel, below the confluence of the Buffalo River, ranged from 22 to 28°C in the summers of 1965 and 1966. During the same time the northern part of the main channel had water temperatures ranging from 11.5 to 24°C.

RESULTS AND DISCUSSION

Distribution of Fishes in the Buffalo River

Black (1940) recorded 26 species from the Buffalo River at six localities from the extreme headwaters, near Mossville in Newton County, to near Gilbert in Searcy County (about river mile 49). All but one of those species, the steelcolor shiner, *Notropis whipplei*, were collected during our study. Fifty-six species, representing 12 families, were collected during our survey.

During the summers of 1965 and 1966, and on subsequent visits to localities in the headwaters sections above Ponca and Parthenon (Stations 15 and 17), the flow of the Buffalo and Little Buffalo branches was found to be intermittent. Black (1940), however, reported 14 species from the headwaters of the Buffalo near Mossville (Station 19). The creek chub, *Semotilus atromaculatus*, was the only one of these not found to occur throughout the length of the river to its confluence with the White River, a distance of over 130 miles. Collections made during our study in the upper section of the river (Stations 14-18), yielded 38 species of fishes, including seventeen cyprinid species. Thirty-five of those species were also taken in

collections throughout the river down to the mouth. Four of the 38, the southern redbelly dace, *Phoxinus erythrogaster*, the creek chub, *S. atromaculatus*, the strippled darter, *Etheostoma punctulatum*, and the orangethroat darter, *E. spectabile*, appeared to be restricted to the headwaters or to small, springfed tributaries to the main river. The occurrence of these species in the main channel was usually associated with the mouth of a small stream. The central stoneroller, *Campostoma anomalum pullum*, was most frequently encountered in such habitats. It was also found, however, throughout the main river, occurring syntopically with the largescale stoneroller, *C. oligolepis*.

Twenty-three of the 56 species collected during our study were taken at all, or all but one, of the 18 sites. Six additional species, the striped shiner, *Notropis chrysocephalus*, the rosyface shiner, *N. rubellus*, the telescope shiner, *N. telescopus*, the slender madtom, *Noturus exilis*, the blackspotted topminnow, *Fundulus olivaceus*, and the banded sculpin, *Cottus carolinae*, presumably exhibit an equally continuous distribution pattern, but were missing from at least two or more successive localities. The hiatus in their distribution can be more satisfactorily explained as due to inadequate collecting, rather than as representative of any true break in the longitudinal distribution of these species.

Six species were found only in the lower reaches of the Buffalo River (Stations 1-4). These were the gizzard shad, *Dorosoma cepedianum*, the highfin carpsucker, *Carpiodes velifer*, the river redhorse, *Moxostoma carinatum*, the channel catfish, *Ictalurus punctatus*, the American eel, *Anguilla rostrata*, and the mottled sculpin, *Cottus bairdi*. Probably only the mottled sculpin is truly restricted to this region. Monthly collections from sites farther upstream would almost certainly include young or seasonally migrating adults of the other five species.

The overall distribution pattern of the Buffalo River fishes appears to be one of species addition, rather than species replacement. Faunal diversity increased rather rapidly from the uppermost site of Black (Station 19), with 14 species, to sites further downstream, where streamflow was uninterrupted and the river channel was noticeably larger, with 38 species. Faunal additions occurred more slowly, but regularly, for the next 56 miles (Stations 13-5), with 12 new species taken to raise the total to fifty. The most diversity was encountered in a very short section of the river, from river mile 8 to the mouth. In this region, 52 species were collected, and six additions were made to the species total.

Five species occurring in the cold tailwaters of the White River, above its confluence with the Buffalo River, may be present in the Buffalo River as well. Two, *Salmo gairdneri*, the rainbow trout, and *S. trutta*, the brown trout, are introduced. The threadfin shad, *D. petenense*, has been successfull stocked in Bull Shoals reservoir (Pflieger, 1971), and appeared in a few collections made below the dam in 1965. *Pimephales promelas*, the fathead minnow, has been used as a bait species throughout the Ozarks (Pflieger, 1971), and two specimens were taken in the White River near Cotter, Arkansas, in 1965. On one occasion, a black crappie, *Pomoxis nigromaculatus*, was collected by electroshocking in a backwater pool off the main White River, within 250 yards of the mouth of the Buffalo River. In addition, the steelcolor shiner, *Notropis whipplei*, has been reported from the Buffalo River near Gilbert, Arkansas (Black, 1940; Gibbs, 1963), though no specimens were collected during the course of this study, and Neil Douglas (pers. comm.) has found a population of golden shiner, *Notemigonus crysoleucas*, in Big Creek, a tributary to the upper section of the Buffalo River. Buchanan (1973) reported *Percina maculata* from two localities bringing the confirmed species total for the Buffalo River to fifty-nine.

The Buffalo River is wholly contained within the Ozark Upland physiographic province. Changes in gradient, substrate, stream size, and other physical features are fairly gradual from headwaters to the mouth. Sharp breaks in the

physical features of the river are minimal. The pattern of species diversity and distribution is not unlike that reported for many other free-flowing, unpolluted streams (Sheldon, 1968; Hynes, 1970; Jenkins & Freeman, 1972).

Selected Species Accounts

As mentioned above, the pattern of distribution in the Buffalo River is generally one of species addition. However, in at least three cases, replacement of headwater species by related forms farther downstream was noted. These involved *Campostoma a. pullum* and *C. oligolepis*; *Etheostoma spectabile* and *E. caeruleum*; and *Cottus carolinae* and *C. bairdi*.

Campostoma.—The occurrence of the largescale stoneroller, *C. anomalum oligolepis* Hubbs and Green, together with the central stoneroller, *C. a. pullum* (Agassiz), was first reported in the White River system in Arkansas by Black (1940). More recently, Pflieger (1971) recognized *C. oligolepis* as a full species based on a number of morphometric and meristic characters. This has been confirmed by Burr and Smith (1976).

The distribution of the central and largescale stonerollers in the Buffalo River was very similar to that reported by Pflieger (1971) for stonerollers in Ozark streams in Missouri. Both species occurred in similar habitats, but *C. a. pullum* showed a distinct preference for smaller streams. In the headwaters and in the smaller tributary streams, the central stoneroller was more numerous, often to the exclusion of the largescale stoneroller. At two upstream sites, the Little Buffalo branch near Jasper (Station 14) and the Buffalo branch near Ponca (Station 17) the ratio of *C. a. pullum* to *C. oligolepis* was about 5 to 3. Downstream from the confluence of the two branches the proportion changed, with the largescale stoneroller outnumbering the central stoneroller by more than 2 to 1.

Etheostoma.—Almost total replacement occurred between the two closely related darter species of the subgenus *Oligocephalus*. The rainbow darter, *E. caeruleum*, is extremely abundant in riffles, over gravel and rubble substrates, in the larger streams of the White River system in the Ozark Uplands. During our survey in the summers of 1965 and 1966 in the main Buffalo River over 800 *E. caeruleum* were collected, but not one specimen of *E. spectabile* was taken. In the lower reaches of the river, where monthly collections were made for 14 months, nearly 2,000 specimens of rainbow darters were collected by electroshocking, but the orangethroat darter was absent. Literature records for *E. spectabile* in the Buffalo River drainage (Black, 1940; Hubbs and Strawn, 1957; and Distler, 1968) convinced us that the species was common and fairly widely distributed in the drainage. Collections by Douglas and Guidroz in a number of smaller tributary streams have yielded large series of *E. spectabile*, which we have examined.

Cottus.—The banded sculpin, *C. carolinae*, was distributed throughout the Buffalo River drainage almost continuously from headwaters to the mouth. It was the only species of sculpin collected by us from river mile 108 to mile 2, where it was often quite common. At the lower two stations, mile 2 and mile 0, the mottled sculpin, *C. bairdi*, greatly outnumbered *C. carolinae* (Table 3), and in the cold tailwaters of the White River, the mottled sculpin virtually replaced the banded sculpin (Brown *et al.*, 1967). Pflieger (1971) noted that the habitat requirements for the two species were very similar, but that *C. carolinae* tended to inhabit the larger, warmer Ozark streams, whereas *C. bairdi* preferred the smaller creeks and spring branches. Black (1940) reported that the White River was the most unchanged of all Arkansas streams. He also indicated that *C. carolinae* was by far the more common of the two species of sculpin in Ozark waters. From his account it appears that the banded sculpin was predominant in the upper White River and that it was the only sculpin collected in the Buffalo River. The construction of three large hydroelectric dams on the Upper White River has brought about numerous changes in the physical and chemical

Table 3. Station by station totals for *Cottus* in the Buffalo River for the summers of 1965 and 1966.

	18	17	16	14	13	12	10	9	8	6	5	3	2	1
Cottus carolinae	2	17	5	65	0	0	0	376	0	4	0	0	7	5
Cottus bairdi	0	0	0	0	0	0	0	0	0	0	0	0	5	239

characters of the river. Quite likely, the severe alteration of water temperature of the tailwater section of the Upper White River has created extensive habitat for *C. bairdi*. Perhaps, in the winter months when the water temperatures of the Buffalo River were even colder than those of the White, the mottled sculpin entered the lower section of Buffalo and became well established there.

Ambloplites.—Pflieger (1971) noted the striking color pattern of Upper White River rockbass. The genus *Ambloplites* is currently being studied by the senior author, who regards the form as warranting specific recognition.

Comparison with the White River

The construction of a series of impoundments on the upper White River in northwestern Arkansas and southwestern Missouri has severely altered the physical and chemical conditions of the effluent. The normal distributions of many species of fish and aquatic invertebrates have likely been affected. Pre-impoundment data, as such, for the area now inundated by Bull Shoals reservoir are not available. However, the extent of the disruption may be inferred by reviewing studies on unimpounded sections of the upper White above Bull Shoals Dam.

Knapp (1958) and Keith (1964) reported 70 and 72 species of fish, respectively, in pre-impoundment studies in free-flowing sections of the upper White drainage in Arkansas and Missouri. Brown *et al.* (1967) found only 24 species in a twenty mile cold tailwater section below Bull Shoals Dam to above the mouth of the Buffalo River. Since 52 of 59 Buffalo River species are known to occur in the region of the confluence, the Buffalo River can be viewed as an important source of species enrichment for the impoverished tailwater fauna of the upper White River.

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SYSTEMATICS OF THE COMMON KINGSNAKE, *LAMPROPELTIS GETULUS* (LINNAEUS) 1

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ABSTRACT

The genus *Lampropeltis* and the species *L. getulus* are defined and relationships are discussed. Individual, ontogenetic, sexual and geographic variation have been analyzed in *L. getulus*. The degree of differentiation among all populations enables the recognition of local populations, microgeographic races, subspecies and subspecies complexes within *L. getulus*. Three subspecies complexes are recognized on the basis of pattern, hemipenial morphology, and intergradation—the *getulus* complex, the *splendida* complex, and the *californiae* complex.

Four subspecies are recognized within the *splendida* complex—*L.g. splendida, L.g. nigritus, L.g. holbrooki,* and *L.g. niger.* Three microgeographic races of *L.g. holbrooki* are distinguished on the basis of pattern. *L.g. splendida* is considered to be closest to the ancestral stock of the species. *L.g. nigritus* is an immediate derivative of *L.g. splendida* by a melanistic reduction in pattern. *L.g. holbrooki* differentiated from the primitive *L.g. splendida* stock by a reduction in the number of dorsal scale rows, and *L.g. niger* evolved from *L.g. holbrooki* by a process of pattern neoteny.

Within the *getulus* complex, two subspecies are recognized—*L.g. getulus* and

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L.g. floridana. A wide zone of intergradation exists in central Florida between the two subspecies as a result of Pleistocene displacement of populations. A disjunct population of *L.g. floridana* occurs in northeastern Florida. The populations in the Apalachicola region of Florida (*L.g. goini*) and the Outer Banks of North Carolina (*L.g. sticticeps*) are considered to be relict intergrades between *L.g. getulus* and *L.g. floridana*. Two microgeographic races of *L.g. getulus* are recognized—a piedmont and a coastal form. *L.g. floridana* is considered a direct derivative of primitive *L.g. splendida* stocks based on similarities of pattern and hemipenial morphology, and the presence of 23 dorsal scale rows. I suggest that ancestral *L.g. floridana* utilized the Gulf Coast Migration Route of the Pleistocene to inhabit the southeastern United States. *L.g. getulus* is derived from *L.g. floridana* by reduction of the number of dorsal scale rows and pattern neoteny.

Only one subspecies within the *californiae* complex is recognized—*L.g. californiae*. The populations exhibiting various banded patterns do not show a significant degree of differentiation worthy of nomenclatural recognition. The striped patterned populations in southern California have been shown to be conspecific with the banded populations (Klauber, 1936, 1939, 1944). Similarly, the striped population in southern Baja California (*L.g. nitida*), on the basis of specimens with a mixed pattern of bands and stripes, has the same relationship with the banded population in southern Baja California (*L.g. conjuncta*= *L.g. californiae*). Specimens intermediate between the striped and banded patterns suggest sympatric intergradation as a result of Pleistocene displacement of populations and all forms are considered as belonging to a single diphyletic subspecies, *L.g. californiae*.

Lampropeltis g. brooksi is considered a synonym of *L.g. floridana*; *L.g. goini* and *L.g. sticticeps* are intergrade populations and are considered synonyms of both *L.g. getulus* and *L.g. floridana*. *L. catalinensis* is shown to be a synonym of *L.g. splendida*. *L.g. yumensis*, *L.g. conjuncta*, and *L.g. nitida* are considered synonyms of *L.g. californiae*. No new subspecies are described.

INTRODUCTION

Fifty years have elapsed since the publication of Blanchard's (1921) revision of the genus *Lampropeltis*. For that classical study, Blanchard examined 1,581 specimens of the genus, which he considered to be comprised of three natural divisions (excluding the then poorly known *L. mexicana*), the *calligaster, getulus,* and *triangulum* groups. Within the *getulus* group, Blanchard included two species, *L. getulus* and *L. californiae*, and eleven subspecies: *L.g. boylii, L.g. brooksi, L.g. conjuncta, L.g. floridana, L.g. getulus, L.g. holbrooki, L.g. niger, L.g. splendida, L.g. yumensis, L.c. californiae,* and *L.c. nitida*. Subsequently, additional taxa have been described: *Lampropeltis catalinensis* Van Denburgh and Slevin, 1921; *L.g. sticticeps* Barbour and Engels, 1942; *L.g. goini* Neill and Allen, 1949; and *L.g. nigritus* Zweifel and Norris, 1955. Klauber (1936, 1939, 1944) established that *L.c. californiae* and *L.g. boylii* are polymorphic phases of *L.g. californiae*. Schmidt (1953) included *L.g. sticticeps* in the synonymy of *L.g. getulus* without comment, but Wright and Wright (1957) recognized the subspecies as problematical and Lazell and Musick (1973) considered the taxon valid. Duellman and Schwartz (1958) placed *L.g. brooksi* in the synonymy of *L.g. floridana*. Soule and Sloan (1966) included *L. catalinensis* as a subspecies of *L. getulus* without comment.

Since Blanchard's (1921) revision, there has been no analysis of geographic variation in *Lampropeltis getulus*. The status of *L.g. catalinensis, L.g. conjuncta, L.g. goini, L.g. nigritus, L.g. sticticeps,* and *L.g. yumensis* is questionable. Uncertainty clouds the relationships among *L.g. goini, L.g. floridana,* and *L.g. getulus; L.g. niger* and *L.g. getulus*; *L.g. catalinensis* and all other forms; *L.g. nitida* and *L.g. conjuncta*; and the two pattern phases of *L.g. californiae*. The additional specimens that have become available since 1921 in collections throughout the country have made this study not only possible, but desirable, in

1 This work was completed in partial fulfillment for the degree of Doctor of Philosophy at Louisiana State University, Baton Rouge, Louisiana.

order to clarify the systematics of the species.

METHODS AND PROCEDURES

During the course of this study I examined 2,200 specimens of *Lampropeltis getulus* from the following collections: AMNH-American Museum of Natural History; AS-Albert Schwartz, Private Collection; ASDM-Arizona-Sonora Desert Museum; ASU-Arizona State University; AU-Auburn University; BCB-Bryce C. Brown, Private Collection; BS-Bruce Sutton, Private Collection; CAS-California Academy of Sciences; CA-Chicago Academy of Sciences;CM-Charleston Museum; DU-Duke University; EAL-Ernest A. Liner, Private Collection; EVRC-Everglades National Park Reference Collection; FMNH-Field Museum of Natural History; FSU-Florida State University; INHS-Illinois Natural History Survey; ISM-Illinois State Museum; JTC-Joseph T. Collins, Private Collection; KU-University of Kansas Museum of Natural History; LACM-Los Angeles County Museum; LDO-Lewis D. Ober, Private Collection; LDW-Larry D. Wilson, Private Collection; LSUMZ-Louisiana State University Museum of Zoology; LTU-Louisiana Tech University; MCZ-Museum of Comparative Zoology, Harvard; MSU-Mississippi State University; MVC-Museum of Vertebrate Zoology, University of California; NCSM-North Carolina State Museum; NLU-Northeast Louisiana University; NMSU-New Mexico State University; OSU-Oklahoma State University Museum of Natural and Cultural History; PMB-Philip M. Baker, Private Collection; RAT-Robert A. Thomas, Private Collection; SDSNH-San Diego Society of Natural History; SM-Strecker Museum; TCWC-Texas Cooperative Wildlife Collection, Texas A & M; TNHC-Texas Natural History Collection, University of Texas; TTC-Texas Technological College; TU-Tulane University; UAHC-University of Alabama Herpetological Collection; UAZ-University of Arizona; UCM-University of Colorado Museum; UF-University of Florida, Florida State Museum; UG-University of Georgia; UIMNH-University of Illinois Museum of Natural History; UK-University of Kentucky; UM-University of Miami; UMMZ-University of Michigan Museum of Zoology; UNM-University of New Mexico; USA-University of Southern Alabama; USL-University of Southwestern Louisiana; USM-University of Southern Mississippi; USNM-United States National Museum; UT-University of Tennessee.

In addition to the preserved museum specimens, I examined many living specimens in order to increase my understanding of color and pattern variation.

Dorsal scale reduction formulas were recorded as in Dowling (1951a), beginning one head length posterior to the head and ending one head-length anterior to the vent. Ventral scales were counted in the standard manner following Dowling (1951b). Measurements were made in the following manner: snout-vent length, from the tip of the snout to the posterior margin of the anal plate; tail length, from the posterior margin of the anal plate to the tip of the tail (only specimens with entire tail spines were measured); head length, taken in a straight line from the posterior tip of the lower jaw to the tip of the rostral plate; snout length, taken in a straight line from the anterior margin of the orbit to the tip of the rostral plate. All measurements were made on preserved specimens. Unless otherwise noted in the presentation of scutellation data, the figures in parentheses represent the percentage of the specimens examined possessing that character.

Drawings of midbody patterns are composite because it is not possible to depict all pattern variations. Dorsal bands were counted on the body only, beginning one head length posterior to the head and terminating above the vent.

GENUS *LAMPROPELTIS* FITZINGER

Lampropeltis Fitzinger, 1843: 25. Type species, *Herpetodryas getulus* Schlegel.

Sphenophis Fitzinger, 1843: 25. Type species, *Coronella coccinea* Schlegel = *Lampropeltis triangulum* (Lacépède).

Ophibolus Baird and Girard, 1853: 82. Type species *Herpetodryas getulus* Schlegel.

Osceola Baird and Girard, 1853: 133. Type species, *Calamaria elapsoidea* Holbrook = *Lampropeltis triangulum* (Lacépède).

Bellophis Lockington, 1876: 52. Type species, *Coluber zonatus* Blainville.

Oreophis Duges, 1897: 284. Type species, *O. boulengeri* Dugès = *Lampropeltis mexicana* (Garman).

Triaenopholis Werner, 1924: 50. Type species, *T. arenarius* Werner = *Lampropeltis getulus* (Linnaeus).

Definition.—A genus of colubrid snakes with smooth lanceolate dorsal scales in 17 to 27 rows, each scale with 2 apical pits, equal in size except for the slightly enlarged ones in the first or first and second rows; head not or only slightly distinct from neck; eye moderate in size

with a round pupil; nasal divided; ventrals not angular; anal plate entire; subcaudals normally divided; tail moderately long; maxillary teeth 12 to 20 and ungrooved; dentary teeth 12 to 18; palatine teeth 8 to 14; pterygoid teeth 12 to 23; hemipenes clavate or bilobed, calyculate apically, spinose on lower distal half, basal half naked or with minute spines, sulcus spermaticus single.

LAMPROPELTIS GETULUS (LINNAEUS)

Coluber getulus Linnaeus, 1766: 382.
Coluber eximis: Harlan, 1827: 360. Misapplication of *C. eximis* Dekay, 1842 = *Lampropeltis t. triangulum.*
Coluber californiae Blainville, 1835: 292.
Coronella sayi: Holbrook, 1842: 99. Misapplication of *Coluber sayi* Schlegel, 1837 = *Pituophis melanoleucus sayi.*
Ophibolus boylii Baird and Girard, 1853: 82.
Ophibolus splendida Baird and Girard, 1853: 83.
Coronella balteata Hallowell, 1853: 236.
Coronella pseudogetulus Jan, 1863: 238, 247.
Lampropeltis conjuncta: Van Denburgh, 1895: 142.
Lampropeltis nitida Van Denburgh, 1895: 143.
Lampropeltis holbrooki Stejneger, 1903: 152.
Lampropeltis boylei: Atsatt, 1913: 41.
Lampropeltis catalinensis Van Denburgh and Slevin, 1921: 397.
Triaenopholis arenarius Werner, 1924: 50. Based on a bleached specimen without data (M.A. Smith, 1928).

Holotype.—None designated. Type locality originally given as "Carolina" but Klauber (1948) restricted it to the vicinity of Charleston, South Carolina.

Definition.—A medium to large-sized (to 2083 mm) species of *Lampropeltis* characterized by a tail 10.8 to 15.3% of total length in males, 9.2 to 14.7% in females; temporals normally 2 + 3; oculars 1 + 2; loreal usually present; supralabials usually 7; infralabials 9 or 10; intergenials 1 + 2, 2 + 2, or 2 + 3; dorsal scales in 19 to 25 rows at midbody; ventrals 197 to 250 in males, 198 to 255 in females; subcaudals 44 to 63 in males, 37 to 57 in females; teeth 12 to 16 on each maxilla, 14 to 17 on each dentary, 8 to 11 on each palatine, and 12 to 20 on each pterygoid; hemipenis slightly to distinctly bilobed; dorsal pattern highly variable, but basically consisting of a black to chocolate brown ground color, often with some or all of the scales light or light centered (white, cream, or occasionally reddish yellow), frequently forming distinct crossbands or sometimes longitudinal stripes; venter also highly variable, ranging from uniformly dark to uniformly light.

Range.—North America, from the Atlantic Coast below the 41st Parallel to the Pacific Coast below the 43rd Parallel, and south into Mexico to Zacatecas and San Luis Potosi, and most of the Baja California peninsula (conspicuously absent from Colorado, the northern one-third of New Mexico, northeastern Arizona, most of Utah, and northeastern Nevada); vertical range from sea level to about 2,100 m.

Relationships.—*Lampropeltis getulus* is a generalized snake that represents one of probably four lines of radiation from a primitive stock closely allied to the group of colubrine genera that includes *Pituophis* and *Elaphe*. On the basis of fossil records (see p. 97), I suggest that this radiation occurred during the early Pliocene. Further, on the basis of the presence of characters considered to be primitive within the species, I consider northern Mexico and the adjacent south-central United States to be the area where this radiation initially occurred. This centrally located region offers the greatest theoretical potential for derivation of most populations of *L. getulus* and other species in the genus.

The species most closely related to *Lampropeltis getulus* is *L. calligaster* which differs only in pattern, the latter being a distinctly blotched snake. Both of these species differ from members of the *triangulum* and *mexicana* groups of kingsnakes in not having the posterior two maxillary teeth enlarged. However, Webb (1961) suggested that on the basis of similarity in color pattern, *L. calligaster* might be a derivative of the *mexicana* group. He further stated that *L. getulus* might be a derivative of *L. calligaster,* although "no living forms indicate relationships." This line of reasoning based on a single character state is unwarranted. Although I do regard the blotched pattern as more primitive than

the speckled, banded, or striped patterns exhibited by *L. getulus*, I suggest that the pattern of *L. calligaster* represents retention of a primitive character, and that the pattern of *L. getulus* is a specialization. *L. calligaster* exhibits such specializations as reduced head size and, in *L.c. rhombomaculata*, as reduced scutellation (dorsal scale rows, infralabials); these are modifications for a more fossorial existence.

I suggest, therefore, that the initial radiation of *Lampropeltis* consisted of two lines of divergence, the *getulus* and *triangulum* groups. The *getulus* group differentiated into *L. getulus* and *L. calligaster* whereas *L. triangulum, L. pyromelana, L. zonata,* and *L. mexicana* evolved from the primitive stock of the *triangulum* group.

Fossil history.—Pleistocene fossils of *Lampropeltis getulus* have been reported from various localities in Florida (Auffenberg, 1963; Brattstrom, 1953a; Holman, 1958), Texas (Holman, 1964a), Nebraska (Holman, 1964b), Nevada (Brattstrom, 1954), and California (Brattstrom, 1953b and c). These widely separated localities suggest that the species has been in existence for a considerable length of time, at least during the entire Pleistocene and probably back into the Pliocene. The genus is represented in the Pliocene of Nebraska, Kansas, Oklahoma, and Michoacan, Mexico (Brattstrom, 1955 and 1967; Holman, 1964a).

VARIATION

Individual Variation.—The degree of individual variation within a closely interbreeding population is usually quite small. For example, in the number of ventral scales, the range of variation within a single population usually does not exceed 12 scales (*i.e.*, 201-211 for 10 males from Cameron Parish, Louisiana; 201-212 for 25 males from the vicinity of New Orleans, Louisiana).

Supralabials usually are 7 (97.1%), but a few individuals have 8 (2.5%) or 6 (0.4%). Infralabials are somewhat less consistent and some geographic variation is noted, but 9 is the most frequently encountered number (80.8%), sometimes 10 (17.5%), rarely 8 (1.3%) or 11 (0.4%). Temporals are normally 2 + 3 (94.5%) but aberrant individuals may possess 2 + 2 (2.0%), 2 + 1 (0.05%), 2 + 4 (1.9%), 3 + 3 (0.05%), 3 + 4 (0.7%), 1 + 2 (0.4%), or 1 + 3 (0.3%). Oculars are the most consistent scales in that 99.3% of the specimens examined possess 1 + 2, but formulas of 1 + 3 (0.3%), 1 + 1 (0.2%), or 2 + 2 (0.2%) do occur. The loreal is normally present, but in an occasional specimen the scale may be absent on either or both sides of the head. This condition most often results from fusion of the loreal with the supraocular, preocular, or postnasal, but in 2% of the specimens examined, no loreal was found and no evidence of fusion was noted. Usually, the postnasal and preocular extend to fill in this area. Many individuals were found in which the loreal was represented by a greatly reduced, almost granular scale. A female specimen (KU 74114 from Cumberland County, Tennessee) lacks the loreal on both sides, and within her brood of seven, four specimens also lack the loreal scale. This evidence indicates that a single allele may be responsible for the absence of a loreal scale. All specimens examined, except one, possess a single anal plate.

There is considerable individual variation in proportional characters. Relative tail length varies from the mean by several per cent in every sample. Head length as a percentage of snout-vent length varies within about one-half per cent of the mean for any given length (Fig. 1). The range of variation of snout length relative to head length is as much as $\pm$ 7% from the mean (Table 1). Some of this variation is undoubtedly due to the inherent difficulty of measuring preserved snakes.

Ontogenetic Variation.—Character changes from the juvenile to the adult can be detected in relative head length, to a lesser degree in relative tail length, and, in some areas, in pattern.

Marked differences are found in head length of newly hatched individuals (up to 5.7% of snout-vent length), when com-

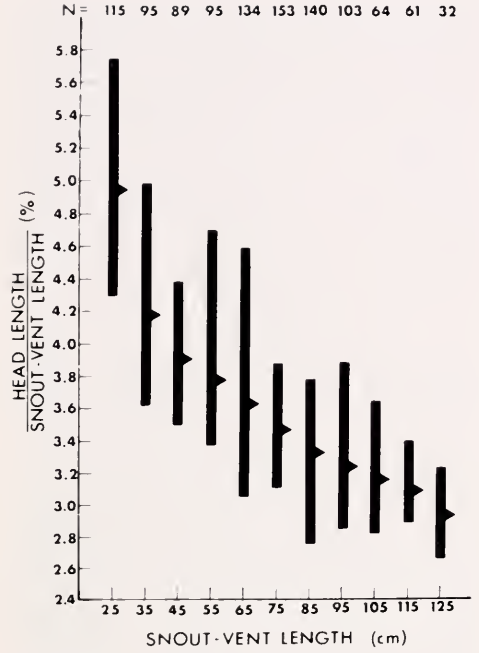


Figure 1. Ontogenetic variation in head length expressed as a percentage of snout-vent length in *Lampropeltis getulus*. The mean for a sample of any given snout-vent length is indicated by a point on the sample range.

pared with adults (as little as 2.7% of snout-vent length). This condition is apparently due to allometric growth of the body and the head (Fig. 1).

Tail length varies ontogenetically only slightly. Newly hatched individuals tend to have slightly longer tails, and very large adults (>1150 mm) tend toward a proportionally shorter tail, but the differences are within the extremes of individual variations at any length.

Ontogenetic pattern variation is found in certain geographic areas. In the central and eastern portion of the range (southern Iowa to eastern Texas east to Ohio to northwestern Georgia and Alabama), juveniles have distinct light dorsal bands on a dark background with little or no spotting between the bands. As the individual matures, one of two changes occurs. In the western portion of the area outlined above, some or all of the dorsal scales develop a light center which I shall refer to as secondary spotting. This secondary spotting may completely obscure the juvenile dorsal bands (especially in Missouri, western Arkansas, eastern Oklahoma, eastern Texas, and portions of Louisiana), or they may remain evident. In the eastern portion of this range (Illinois, Indiana, Ohio south to northeastern Alabama and northwestern Georgia), the reverse ontogenetic change occurs. The juvenile pattern becomes reduced in the adult, sometimes resulting in an almost complete loss of any evidence of dorsal bands or secondary spotting, leaving a black dorsum with the minute spots on some scales forming vague dorsal bands.

In the southern half of the Florida peninsula, individuals exhibit a similar form of ontogenetic pattern variation. Juveniles are patterned with distinct dorsal bands, 1.5 to 4 scales long, which usually do not reach the first or second scale row, often ending abruptly or sometimes forking laterally and joining neighboring bands. As the animal matures, scales between the dorsal bands develop a light spot at the anterior end. These secondary spots expand until the entire scale, except the most posterior edge, is light colored. The juvenile pattern may be completely obscured in the adult.

Sexual Variation.—Sexual dimorphism is found in several characters. In some populations, there is a difference between males and females in the number of ventral scales. In about half of these populations, the female has a slightly higher number; in the other populations, the reverse is true. The average difference between males and females is never more than five ventral scales. Many populations, especially in extreme southeastern United States, exhibit no sexual variation in this character.

Subcaudals vary sexually, with females having consistently fewer, although the degree of difference varies geographically. Similarly, females possess a proportionally shorter tail than males.

Table 1. Sexual and geographic variation in snout length expressed as a percentage of head length. Numbers in parentheses indicate range of variation.

Geographic range	males	females
Southern Florida	31.3 (29.6—33.8) N = 17	30.7 (29.3—32.6) N = 19
Virginia to New Jersey south to northern Florida	29.9 (26.8—34.0) N = 109	29.9 (26.7—33.1) N = 62
Illinois to Ohio south to northern Alabama and northwestern Georgia	30.2 (27.0—32.3) N = 43	31.1 (29.4—33.6) N = 20
Southern Iowa south to eastern Texas, Louisiana, Mississippi and western Alabama	30.4 (27.7—34.0) N = 145	30.9 (28.4—34.2) N = 105
Eastern Arizona east to western Texas and south through Mexico	30.5 (27.9—32.2) N = 36	31.2 (29.4—33.2) N = 16
Oregon, Nevada, Utah south to western Arizona and Baja California	31.1 (27.9—33.7) N = 114	30.7 (28.3—33.8) N = 97

Snout length relative to head length varies to some extent sexually and geographically (Table 1). All of these figures, however, may be of little significance because of the amount of individual variation. Head length does not vary sexually.

Geographic Variation.—Geographic variation is found in the number of ventrals, subcaudals, infralabials, intergenials, and dorsal scale rows, the size and shape of the loreal, the relative size of the anterior and posterior genials, color pattern, and structural features of the hemipenes. Proportional characters also vary geographically, but their significance is slight.

Ventrals—The geographic variation of ventral scales is summarized in Figs. 2a, 2b and 3. In general, the greatest number of ventrals is found in southern California and Baja California (213-255), the number decreasing to the north and east. Areas in which the snakes have a low number of ventrals are in the Chihuahuan Desert of Mexico (199-216); western Louisiana, southeastern Texas, Arkansas, eastern Oklahoma, eastern Kansas, Missouri, Illinois, Indiana, Ohio, Kentucky, and Tennessee (197-214); and the extreme northeastern coastal portion of the range, including the islands off North Carolina (200-211). Over the remainder of the range of the species, the range of variation is between 210 and 225.

A series of specimens from Mexico is problematical. The majority of specimens examined from Durango, Zacatecas, and San Luis Potosí have a low number of ventrals (200-205). Two specimens, however, have an unusually high number of ventrals. A female from 29 miles NE of Ciudad Durango (EAL 1850) has 237 ventrals compared with a male from 5.1 miles east-southeast of Durango (UMMZ 114654) which has only 203 ventrals. Similarly, a male from 4.6 miles S of San Lorenzo, San Luis Potosi (EAL 552) has 227 ventrals, whereas four

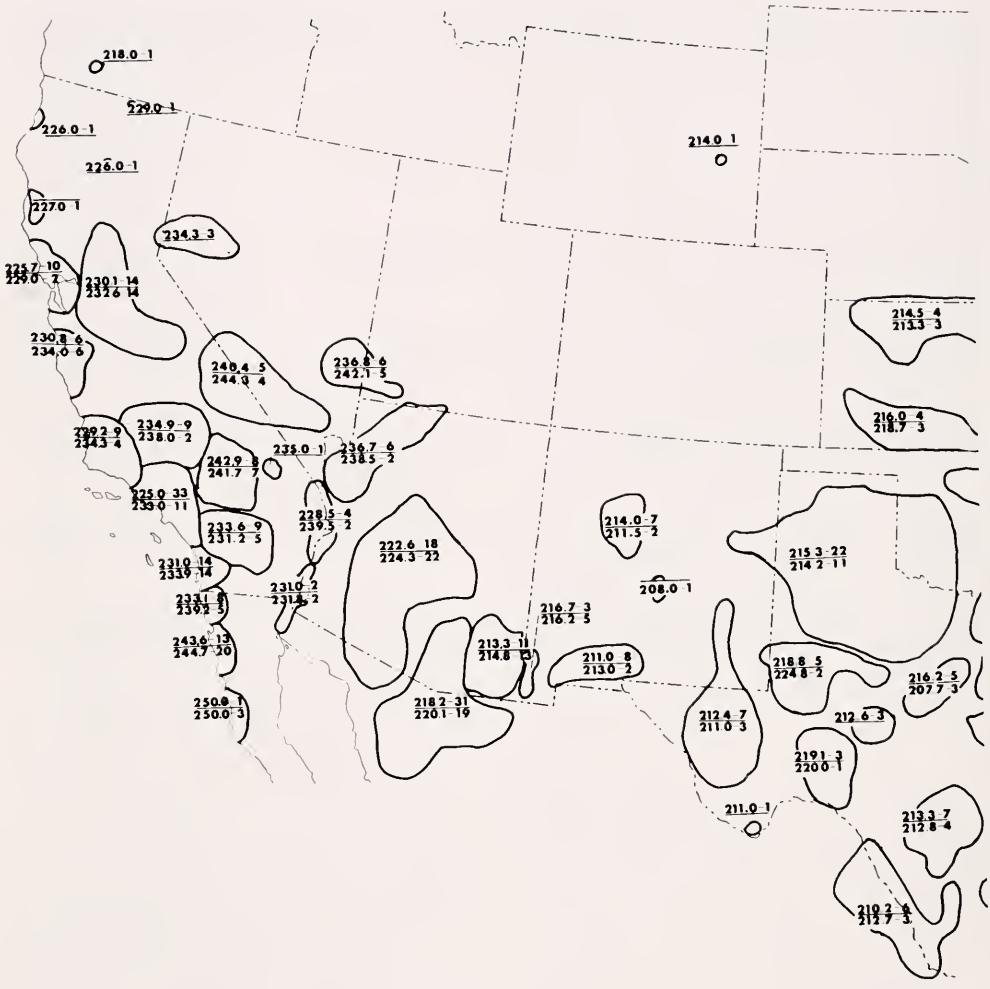


Figure 2a. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in the western United States. The upper figures associated with each sample represent the mean and the sample size (separated by a dash) for males; lower figures present the same data for females. Data are not indicated separately when the mean for males and females is identical.

specimens from nearby localities have between 200 and 205.

Subcaudals—Geographic variation in subcaudal number is shown in Figs. 4 and 5. The amount of individual variation is greater than the geographic variation, but certain tendencies are noted. Specimens with the greatest number of subcaudals are found in the western United States where the maximum is 63 in males and 57 in females. The averages range from 52.6 to 57.2 in males and 48.0 to 52.7 in females. The average number of subcaudals reduces to a low of 46.2 in males and 40.5 in females in the northeastern part of the range (Maryland and Delaware). Clinal variation is noted in the Atlantic coastal populations, where there is a general increase from north to south. The New Jersey population,

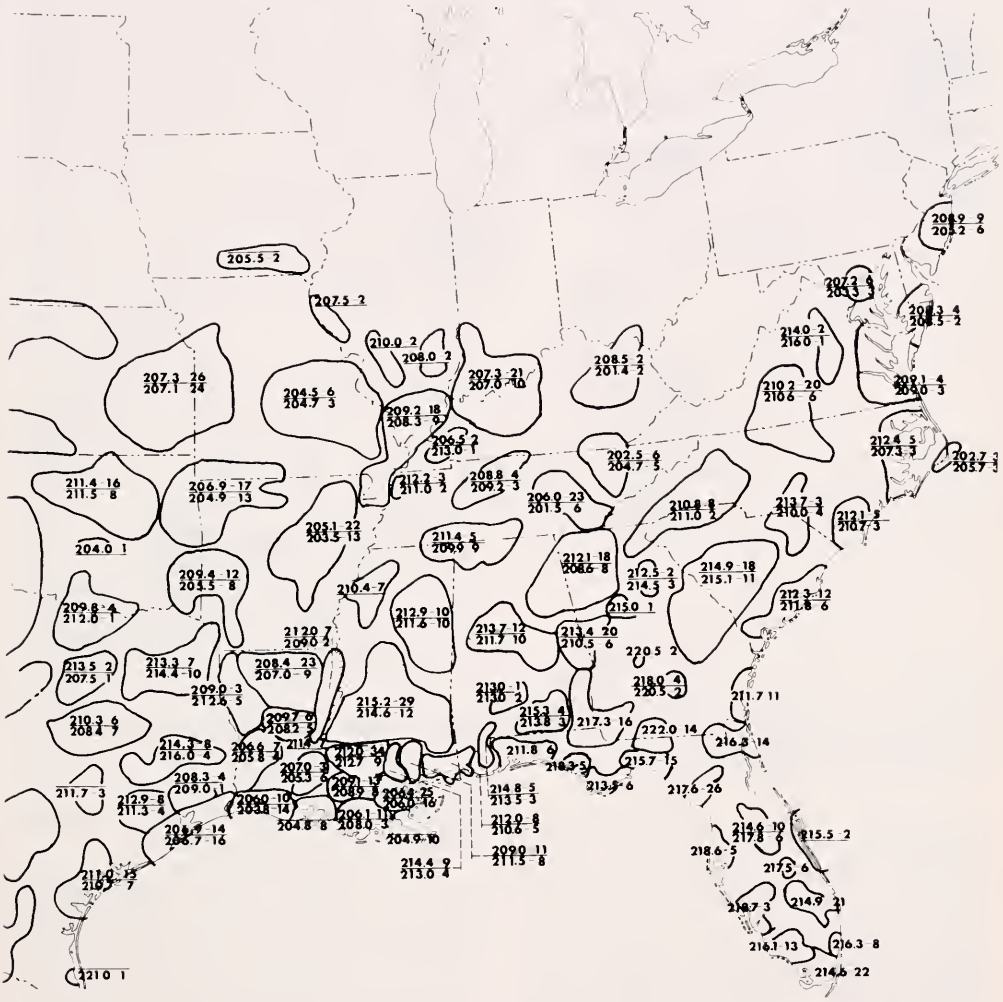


Figure 2b. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in the eastern United States. Explanation as for Figure 2a.

however, is unusual in that the males average 2.9 subcaudals more than the Maryland and Delaware populations; females 2.1 subcaudals more.

Surprisingly, there is no correlation between the number of subcaudals and relative tail length. The western populations, despite having a higher number of subcaudals, have about the same tail length/total length ratio as the remaining populations. The differences in number that do exist appear to be determined by the size of the subcaudal scales, not by the length of the tail.

Infralabials—Among eastern and central populations, infralabials vary individually. The majority of specimens have 9 (80 - 90%), the remainder 10 (10 - 20%) or rarely 8 or 11. In the extreme western portion of the range (Oregon, Nevada, Utah, northern and western Arizona, California, and Baja California), only 66.8% of the specimens examined possess 9 infralabials, while

Figure 3. Geographic variation in the number of ventral plates in *Lampropeltis getulus* in Mexico. See Figure 2 for explanation.

30.8% have 10. The majority of specimens examined from the Baja Peninsula have 10 infralabials: 62.5% from Baja California del Sur; 56.0% from Baja California del Norte. The percentage declines abruptly to only 30.0% in southwestern California (San Diego, Orange, and Los Angeles counties).

Loreal—The shape of the loreal varies individually and geographically. In most specimens, the loreal is square (45.0%), slightly longer than high (10.2%), or slightly higher than long (9.2%). The loreal is considerably longer than high in 18.7% of the specimens examined, and considerably higher than long in 14.9%.

Geographic variation in loreal shape is summarized in Table 2. The most apparent geographic tendencies are seen in peninsular Florida where 71.0% of the specimens examined have a loreal that is higher or slightly higher than long, whereas this condition prevails in only 46.0% of the specimens in Atlantic coastal populations. By comparison, however, fewer specimens from adjacent areas have a high loreal.

In the extreme western United States and Baja California, the loreal is usually slightly longer or much longer than high (60.0%). In New Mexico, western Texas, and Central Mexico, only 44.7% of the specimens have a long loreal. In southern Arizona and adjacent Mexico, however, only 32.2% of the specimens have a long loreal.

Genials—The relative size of the genials varies geographically. In Atlantic coastal populations, the anterior and posterior genials are usually equal in length (62.3%), or the anterior genials are only slightly longer (13.0%) or slightly shorter (9.2%). In central populations, only 31.4% of the specimens examined have genials of equal length, whereas in 46.8% the anterior genials are very much longer than the posterior genials (posterior genial length/anterior genials are slightly longer. Among these central populations, specimens from New

Mexico, eastern Mexico, Texas, western Oklahoma and Kansas have longer anterior genials (54.0%) than the eastern populations (44.1%), with the lowest percentage (32.2%) in Illinois, Indiana, Ohio, Kentucky and Tennessee. In the extreme western states and Baja California, 52.3% of the specimens examined have the anterior genials much longer than the posterior, and in another 26.3% the anterior genials are slightly longer. In only 21.2% of the specimens are the genials equal.

Intergenials—The relative size of the genials is correlated with the number of intergenials. Among eastern populations, most individuals have a combination of 1 + 2 intergenials between the posterior genials (82.0%) with most of the remaining having only 2 intergenials (10.4%). Genials in these specimens are generally about equal in length.

Specimens from western Texas, New Mexico, eastern Arizona, and Mexico (except Baja California) usually have an intergenial arrangement of 2 + 2 (62.0%) or 2 + 3 (22.2%), the latter being especially true in the western-most areas. Individuals from central and northern Texas, western Oklahoma, and Kansas are variable in that 59.4% of the specimens examined have 1 + 2 intergenials, 35.5% have 2 + 2, and 3.9% have only 2. The specimens with a greater number of intergenials normally have short posterior genials.

Pacific coastal states and Baja California populations normally have 2 + 3 (55.0%) intergenials or 2 + 2 (38.0%). Only 1.8% of the specimens examined from those areas have 1 + 2 intergenials.

Dorsal scale rows—The number of dorsal scale rows at midbody varies from 19 to 25 or, rarely, 27. Generally, specimens from east of the Great Plains to the Atlantic coast, except peninsular Florida, have a maximum of 21 dorsal scale rows with typical reductions as follows:

$$21\ \frac{4\ +\ 5\ (111\text{-}177)}{4\ +\ 5\ (116\text{-}176)}\ 19\ \text{or,}$$

$$19\frac{+6\ (25\text{-}63)}{+6\ (25\text{-}63)}21\ \frac{4\ +\ 5\ (111\text{-}146)}{4\ +\ 5\ (116\text{-}145)}19.$$

Occasionally, specimens may reduce to 7 scale rows anterior to the vent:

$$19\frac{+6\ (28\text{-}63)}{+6\ (30\text{-}63)}21\ \frac{4\ +\ 5\ (98\text{-}137)}{4\ +\ 5\ (102\text{-}139)}$$

$$19\ \frac{4\ +\ 5\ (164\text{-}197)}{4\ +\ 5\ (176\text{-}198)}\ 17,\ \text{or}$$

$$21\ \frac{4\ +\ 5\ (100\text{-}140)}{4\ +\ 5\ (101\text{-}138)}$$

$$19\ \frac{5\ +\ 6\ (165\text{-}193)}{5\ +\ 6\ (163\text{-}195)}\ 17.$$

One specimen, LSUMZ 23508 from 2 miles S Holmwood, Calcasieu Parish, Louisiana, has a maximum of only 19 scale rows and reduces to 17 as follows:

$$19\ \frac{4\ +\ 5\ (148)}{4\ +\ 5\ (151)}\ 17\ [206].$$

Rarely, specimens may reach the maximum of 23 scale rows by the addition of a sixth row on each side, as in DU R-293 from 10 miles NW Durham, Durham County, North Carolina:

$$21\frac{+6\ (60)}{+6\ (59)}\ 23\frac{6\ +\ 7\ (103)}{5\ +\ 6\ (109)}$$

$$21\frac{4\ +\ 5\ (176)}{4\ +\ 5\ (178)}\ 19\ [215].$$

In general, those specimens from the western portion of the range outlined above (Kansas south to Texas and east to Ohio south to Alabama) tend to reduce to 19 scale rows farther anteriorly, and more frequently reduce to 17 one head length anterior to the vent than Atlantic coastal specimens, which tend to reduce to 19 scale rows farther posteriorly and rarely reduce to 17. Occasional individuals, for example NCSM 5729 from Raleigh, Wake County, North Carolina, may reduce from 21 to 19 scale rows by the fusion of scale rows 3 and 4 instead of 4 and 5:

$$21\frac{3\ +\ 4\ (159)}{3\ +\ 4\ (161)}\ 19\ [211].$$

Figure 4a. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in the western United States. See Figure 2 for explanation.

Also, occasional specimens will increase from 19 to 21 scale rows anteriorly by the addition of row 5 on both sides, instead of row 6, as, for example, in DU R-29 from 2 to 3 miles N Hillsboro, Orange County, North Carolina:

$$19\ \frac{+5\ (29)}{+5\ (25)}\ 21\frac{4\ +\ 5\ (146)}{4\ +\ 5\ (145)}\ 19\ [212].$$

A posterior reduction to 17 scale rows involves either the fusion of rows 4 and 5 or 5 and 6 and only rarely rows 3 and 4.

In southern Florida, specimens usually have a maximum of 23 scale rows. Anteriorly, the number of scale rows may be 21, as exemplified by an EVRC uncatalogued specimen from Flamingo Campground, Everglades National Park, Monroe County, Florida:

$$21\frac{+6\ (46)}{+6\ (43)}23\frac{5\ +\ 6\ (139)}{5\ +\ 6\ (132)}$$

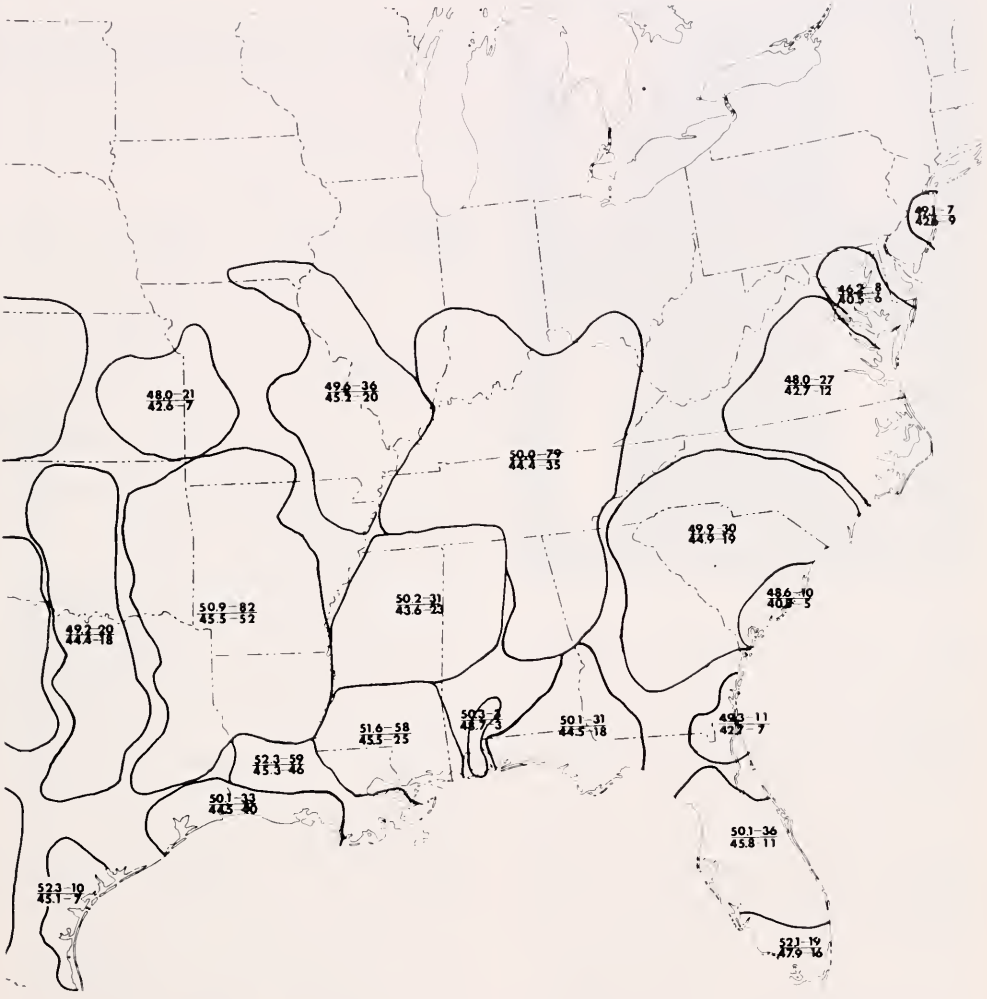


Figure 4b. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in the eastern United States. See Figure 2 for explanation.

$$21\,\frac{4\ +\ 5\ (184)}{4\ +\ 5\ (183)}\,19\ [220],$$

or, may be 23, as in AS 771 from Miami, Dade County, Florida:

$$23\,\frac{5\ +\ 6\ (122)}{4\ +\ 5\ (116)}\,21\ [217].$$

The reduction to 19 scale rows occurs within 40 ventrals of the vent; when the reduction occurs within one head length of the vent it is not included in the reduction formula. The reduction from 23 to 21 rows is usually due to fusion of rows 6 and 7 or 5 and 6, but may be 4 and 5.

Specimens from the western United States and northern Mexico are similar in their scale reductions, but many individuals have a maximum of 25 scale rows, as for example UMMZ 102436 from 4 miles NE Chiricahua, Cochise County, Arizona:

$$25\,\frac{6\ +\ 7\ (137)}{6\ +\ 7\ (138)}\,23\,\frac{5\ +\ 6\ (175)}{5\ +\ 6\ (164)}\,21\ [221].$$

Figure 5. Geographic variation in the number of subcaudals in *Lampropeltis getulus* in Mexico. See Figure 2 for explanation.

Occasional specimens have 27 dorsal scale rows as TCWC 12592 from 3 miles S Navajoa, Sonora, Mexico:

$$25\ \frac{+13\ (73)}{}\ 26\ \frac{12\ +\ 13\ (77)}{}$$

$$25\ \frac{+13\ (83)}{+13\ (102)}\ 27\ \frac{5\ +\ 6\ (136)}{5\ +\ 6\ (136)}$$

$$25\ \frac{12\ +\ 13\ (137)}{11\ +\ 12\ (149)}\ 23\ \frac{6\ +\ 7\ (170)}{5\ +\ 6\ (172)}$$

21 [219].

The final reduction from 23 to 21 scale rows is usually more posterior in the western populations than in Florida specimens; in specimens from California and Baja California, the reduction is even farther posterior than in Texas specimens. This phenomenon is correlated with the higher number of ventral scales found in the extreme western part of the range. For example, TNHC 8348 from 15 miles S Sheffield, Terrell County, Texas, reduces to 21 at the level of ventrals 125 to 130:

$$23\ \frac{+7\ (60)}{+7\ (62)}\ 25\ \frac{5\ +\ 6\ (107)}{5\ +\ 6\ (89)}$$

$$23\ \frac{6\ +\ 7\ (130)}{5\ +\ 6\ (125)}\ 21\ [218],$$

and LSUMZ 10313 from 4 miles S Uvalde, Uvalde County, Texas, which reduces between ventrals 137 and 140:

$$23\ \frac{6\ +\ 7\ (140)}{6\ +\ 7\ (137)}\ 21\ [211].$$

In comparison, CM 55.203.2 from St. George, Washington County, Utah, reduces to 21 rows at the level of ventrals 164 to 166:

$$23\ \frac{6\ +\ 7\ (164)}{5\ +\ 6\ (166)}\ 21\ \frac{4\ +\ 5\ (225)}{4\ +\ 5\ (224)}\ 19\ [244],$$

or, at the lower extreme, UNM 6691 from Santa Rosa, Sonoma County, California, which reduces at ventral 146:

$$23\frac{6 + 7\ (146)}{6 + 7\ (146)}\ 21\frac{4 + 5\ (200)}{5 + 6\ (207)}\ 19\ [222].$$

The kingsnakes from central Texas, western Oklahoma, and Kansas are intermediate between eastern and western populations, individuals in the sample having a maximum of 23 or 21 rows.

Hemipenes.—Hemipenial morphology varies in two respects, overall shape and number of spines on the proximal half. The everted hemipenis is a moderately bilobed structure with the sulcate lobe slightly longer. Male specimens from the Atlantic coastal states, including all of Florida and southeastern Alabama, have deeply bilobed hemipenes with the distal end greatly expanded laterally (Fig. 6,A). This expansion results in a maximum width averaging 75% (68-89%) of the exposed length when fully everted. Throughout the remaining portion of the range of *Lampropeltis getulus*, except the Pacific coastal states of Nevada, Utah, and western Arizona, the hemipenis is not expanded distally, the width averaging 58% (48-68%) of the length. Specimens in the eastern portion of this area (eastern and northern Alabama, Mississippi, Louisiana, Arkansas, eastern Texas, and eastern Oklahoma) have a more clavate organ averaging 52% (49-66%) of the length (Fig. 6,B). Specimens from Texas to southeastern Arizona have a comparatively slightly expanded organ (Fig. 6,C) and the hemipenes of Pacific coastal specimens are moderately expanded (Fig. 6,D).

Throughout most of the range of the species, the basal portion of the hemipenis is naked or ornamented with a few small scattered spines. In eastern Louisiana and southern Mississippi, however, the basal portion of the organs of some individuals is densely covered with minute spines (Fig. 6,B).

Pattern.—The dorsal color pattern is the most significant aspect of geographic

Figure 6. Geographic variation in hemipenial morphology in *Lampropeltis getulus*: A. NCSM 5175 from 4¾ miles NW Laurel Hill, Scotland County, North Carolina; B. Baton Rouge, East Baton Rouge Parish, Louisiana (specimen not available); C. LSUMZ 9995 from 8 miles E Tucson, Pima County, Arizona; D. LSUMZ 9246 from Smoke Creek, Washoe County, Nevada.

variation in *Lampropeltis getulus*. There are three basic patterns with major variations and modifications of these: 1) the speckled pattern, 2) the longitudinally striped pattern, and 3) the banded or "ringed" pattern.

The speckled pattern consists of a dark ground color with each scale on the lateral 8 to 10 rows containing a light central area. Occasional scales in the median 5 to 9 rows are also light-centered with the light spots oriented laterally to form a series of 42 to 97 distinct narrow bands across the dorsal surface (Fig. 7,A). This pattern is found in western Texas, New Mexico, eastern Arizona, and Mexico from Chihuahua and Sinaloa east to Veracruz.

A modified speckled pattern in found in eastern Texas, Louisiana, Arkansas, eastern Oklahoma, Missouri, western Illinois, Mississippi, and southern Alabama. Specimens from this area exhibit a pattern in which every scale, or almost

Table 2. Geographic variation in loreal shape expressed as a percent of specimens examined.

	Loreal Shape:	Square	Slightly longer	Slightly higher	Longer	Higher
New Jersey to Virginia south to northern Florida and southeastern Alabama	N= 211	45.5	1.4	12.3	6.2	33.6
Peninsula Florida	N= 62	27.4	1.6	16.2	0	54.8
Eastern Illinois to Ohio south to northwestern Georgia and northeastern Alabama	N= 112	50.9	3.6	11.6	11.6	17.0
Southern Illinois, extreme western Tennessee, north-central and northwestern Alabama	N= 47	42.6	17.0	23.4	4.3	12.7
Southwestern Alabama, Mississippi, Louisiana, Arkansas, Missouri, eastern Oklahoma, and eastern Texas	N= 316	53.5	8.6	12.3	11.1	12.5
Kansas, central and western Oklahoma, northern and central Texas	N= 130	62.3	9.2	8.5	12.3	7.7
Western Texas west to southeastern Arizona, and south to San Luis Potosi and Zacatecas, Mexico	N= 95	38.4	22.6	7.4	22.1	9.5
South-central Arizona, northern Sonora, Mexico	N= 87	49.4	18.4	4.6	13.8	11.5
Baja California, California, Oregon, Nevada, eastern and northern Arizona, Utah	N= 343	33.1	15.5	3.1	44.5	1.2

every scale, has a centrally located light spot. Some of the dorsal scales may have light spots that are irregularly expanded laterally to form 39 to 94 cross bands (Fig. 7,B). In Illinois, Indiana, Ohio, Kentucky, Tennessee, northeastern Alabama, and northwestern Georgia, the pattern described above is reduced due to ontogenetic loss of the scale spotting. The dorsal bands, consisting of a series of spots, are usually retained, however, although the light centers are often very much reduced (Fig. 7,C).

A similar change occurs in the pattern type found in Sonora, Mexico, which is a reduction of the pattern (Fig. 7,A) found in western Texas, New Mexico, eastern Arizona, and the remaining portions of Mexico. Many of the individuals in this area, especially in southern Sonora, loose all traces of the basic pattern and are uniformly black (Fig. 7,D).

Many specimens from Baja California and California, especially southwestern California, are longitudinally striped. There is usually a continuous light vertebral stripe occupying the vertebral scale row and half of each of the paravertebral rows on a dark ground color. The lateral scale rows, especially rows 1 and 2, are almost completely light, forming lateral stripes (Fig. 7,E). Specimens with this pattern are found sympatrically with banded individuals discussed below.

The third basic pattern consists of light dorsal crossbands on a dark ground color. These bands are usually uninterrupted and not made up of a series of spots as are the bands discussed above (Fig. 7,C). Specimens from the eastern coastal states usually have a pattern of bands which begin on scale row 5 and may be connected with adjacent bands by lateral forking (Fig. 7,F). In southern Florida, this pattern is masked by ontogenetic spotting of the dorsal scales between the light bands (Fig. 7,G).

The banded pattern found in Baja California, California, Oregon, Nevada, Utah, and western Arizona differs in that the bands always extend at least to the first dorsal scale row and usually to the venter (Fig. 7,H).

Geographic variation in the number of dorsal bands occurs in both eastern and western banded populations. In the east, the lowest number of dorsal bands is found among specimens from southern Georgia, southeastern Alabama, and northern Florida (18-22). The number increases clinally both northward and

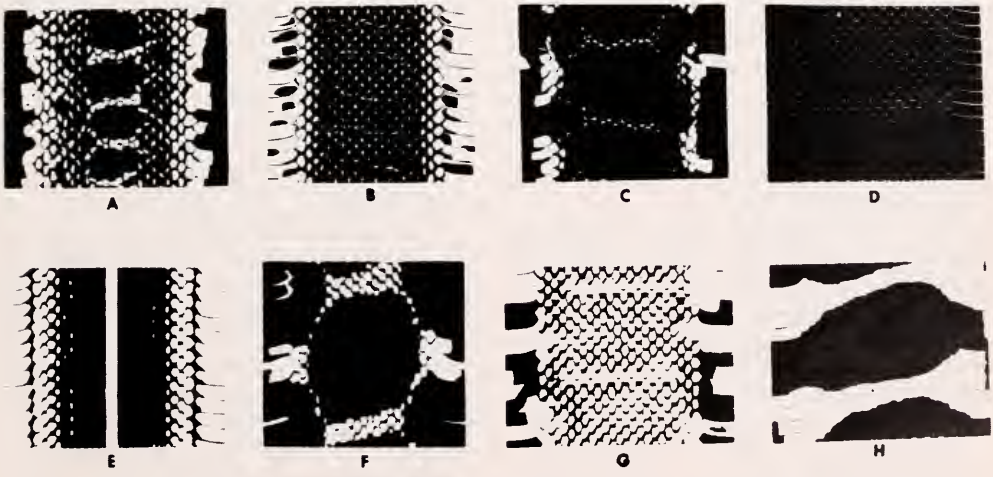


Figure 7. Basic pattern types of *Lampropeltis getulus*. See text (pattern variation) for explanation.

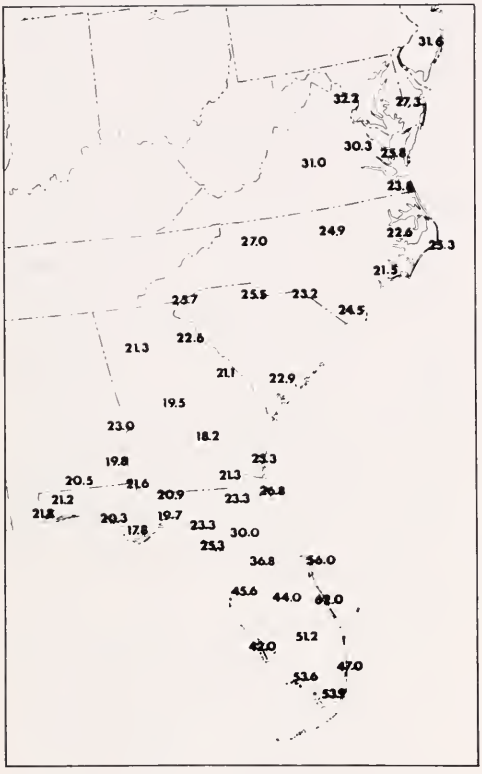


Figure 8. Geographic variation in the number of dorsal body bands in *Lampropeltis getulus* in eastern United States.

southward, increasing to an average of 31.6 in New Jersey, and 53.9 in southern Florida (Fig. 8). In addition, the piedmont populations in North Carolina and Virginia have higher average numbers of dorsal bands (27-32) than coastal populations (21-26).

In the western North American banded populations, the variation in dorsal band number is not as extreme as in eastern populations. Montane populations average generally higher (35-38) than lowland populations (27-30). Clinal variation occurs with the lower numbers in the south, increasing somewhat to the north (Fig. 9).

Non-morphological characters.—Geographical variation in the plasma protein patterns of *Lampropeltis getulus* has been demonstrated by Dessauer and Fox (1958). Specimens from California show a different pattern than a sample from southeastern United States (a mixed sample from Georgia, Mississippi, Louisiana, and Arkansas).

RECOGNITION OF INFRASPECIFIC DIVISIONS

The geographic variation exhibited by *Lampropeltis getulus* in characters of pattern, hemipenial morphology, dorsal scale reduction, loreal shape, intergenial number, and genial size enables the recognition of eight distinct infraspecific divisions, seven of which are allopatric. I recognize these seven allopatric divisions as subspecies of *Lampropeltis getulus*, all of which have available names: *L.g. californiae* (Blainville), *L.g. floridana* Blanchard, *L.g. getulus* (Linnaeus), *L.g. holbrooki* Stejneger, *L.g. niger* (Yarrow), *L.g. nigritus* Zweifel and Norris, and *L.g. splendida* (Baird and Girard). Distribution of these subspecies is summarized in Figs. 10 and 11.

These subspecies exhibit two types of evolutionary relationships to one another. The first is considered to be a primary relationship (*sensu* Eaton, 1970) in which the subspecies have become differentiated but have not entirely lost contact. Where contact still exists, series of demes intermediate in characteristics are found between the adjacent subspecies. Specimens from these populations are considered to be intergrades. Wide zones of intergradation exist between *L.g. getulus* and *L.g. floridana*, *L.g. niger* and *L.g. holbrooki*, *L.g. holbrooki* and *L.g. splendida*, and *L.g. splendida* and *L.g. nigritus*.

Secondary relationships are those in which subspecies have been separated for a long time and have regained contact. A secondary relationship is characterized by a narrow zone of intergradation, as between *L.g. splendida* and *L.g. californiae*, or the occurrence of only occasional intermediates in nature, as between *L.g. getulus* and *L.g. niger*, and between *L.g. getulus* and *L.g. holbrooki*. On the basis of these secondary relationships, the basic pattern types, and hemipenial morphology, three

groups of subspecies can be recognized: the *getulus* complex, consisting of *L.g. getulus* and *L.g. floridana*; the *splendida* complex, consisting of *L.g. splendida, L.g. nigritus, L.g. holbrooki,* and *L.g. niger;* and the *californiae* complex, consisting of only *L.g. californiae*.

KEY TO THE SUBSPECIES OF ADULT *LAMPROPELTIS GETULUS*

1. Maximum number of dorsal scale rows 21 or less.....2
   Maximum number of dorsal scale rows 23 or more.....4
2. Dorsal coloration black or brown with continuous light bands (1 to 10 scales wide) reaching the venter or forking laterally at the level of scale rows 3 to 6, or stopping abruptly at this level; hemipenis deeply bilobed and expanded laterally.....*getulus*
   Dorsal coloration black with some scales centered with yellow, cream, or white; hemipenis not bilobed or much expanded laterally..... 3
3. Most dorsal. scales centered with yellow, cream, or white, the spots on scale rows 6 to 15 sometimes expanded laterally to form narrow light dorsal crossbands.....*holbrooki*
   Dorsum predominantly black, some lateral scales centered with cream or white; often some dorsal scales centered with light pigment to form dorsal bands consisting of a series of spots.....*niger*
4. Light transverse dorsal bands extend laterally to, and often onto, the venter; no spotting between bands.....*californiae*
   Dorsal pattern variable, of longitudinal stripes, spotted scales, or uniformly dark.....5
5. Dorsum dark with a light vertebral stripe and lateral stripes formed by a series of light-centered scales on rows 1 to 3 or 1 to 6; venter usually uniformly light or dark.....*californiae*
   Dorsum without longitudinal stripes.....6
6. Dorsum uniformly black or with only minute light centers on the lateral scales.....*nigritus*
   Dorsum with scales cream or yellow...7
7. Lateral scales with light centers from row one up to row 10; some middorsal scales light centered and expanded laterally to form numerous narrow light bands across the dorsum; occasionally, scales between the bands with light centers producing an entirely spotted dorsum; venter often uniformly dark medially, or blotches; intergenials usually 2 + 2 or 2 + 3; hemipenis not greatly expanded laterally or deeply bilobed.....*splendida*
   Basal portion of each dorsal scale light, posterior edge brown, often each scale completely yellow, dorsal bands of completely light scales often apparent; intergenials usually 1 + 2; hemipenis greatly expanded laterally and deeply bilobed.....*floridana*

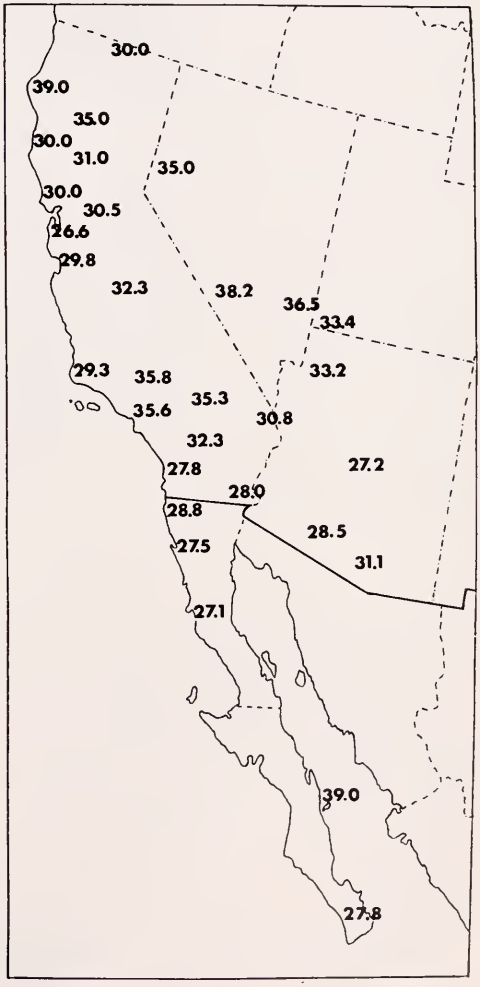
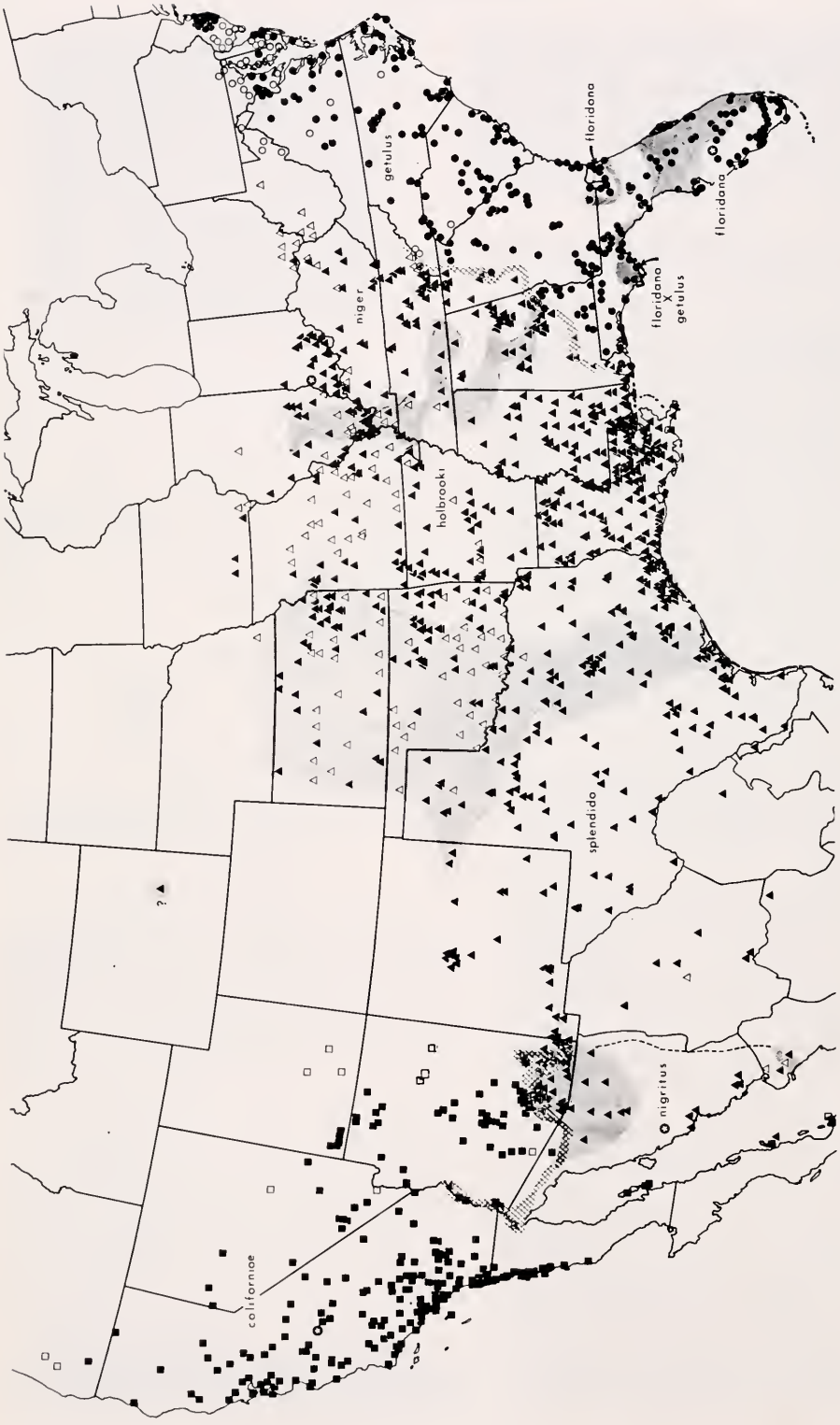


Figure 9. Geographic variation in the number of dorsal body bands in *Lampropeltis getulus* in western United States and Baja California.


floridana
floridana
floridana x gelulus
gelulus
niger
holbrooki
splendidus
nigritus
californiae
?

TAXONOMIC ACCOUNTS
The *getulus* Complex

Lampropeltis getulus getulus (Linnaeus)

Coluber getulus Linnaeus, 1766: 382.
Lampropeltis getulus getulus: Blanchard, 1919: 1.
Lampropeltis getulus sticticeps Barbour and Engels, 1942: 101.
Lampropeltis getulus goini Neill and Allen, 1949: 101.

Holotype.—The data presented for the species apply here.

Definition.—A subspecies of *L. getulus* characterized by 15 to 44 light crossbands on a ground color of chocolate brown to black, a maximum of 21 dorsal scale rows, equal sized genials, 1 + 2 or 2 intergenials, a higher than long or square loreal, and a deeply bilobed and laterally expanded hemipenis.

Range.—Southern half of New Jersey south to northern Florida and west to extreme eastern West Virginia, central Virginia, extreme western North Carolina, the northwestern quarter of Georgia, and southeastern Alabama.

Description.—Ventrals 200 to 223 in males, 201 to 223 in females; subcaudals 45 to 56 in males, 37 to 48 in females; infralabials usually 9 (87.2%), occasionally 10 (11.5%), rarely 8 (1.3%); loreal square (45.5%), slightly higher than long (12.3%), or much higher than long (33.6%), rarely longer or slightly longer than high (6.2% and 1.4%, respectively); intergenials normally 1 + 2 (84.1%) or 2 (11.8%), rarely 1 (2.0%), absent (1.2%), or 2 + 2 (0.9%); anterior genials generally equal to the posterior genials (60.7%), slightly longer (13.3%) or slightly shorter (9.7%), rarely greater (9.7%) or smaller (6.6%); tail length 12.7% (10.9-14.4%) of total length in males, 11.7% (10.1-13.2%) in females; snout length 29.9% (26.8-34.0%) of head length in males, 29.9% (26.7-33.1%) in females.

The color pattern normally consists of white, yellow, or reddish yellow (in young) crossbands on a black, dark brown, or chocolate brown ground color. The bands usually begin on scale row 4 to 8 (patterns 1 and 2, Fig. 13), but in the southern portion of the range, they may extend onto the venter (pattern 3, Fig. 13). These bands often fork anteriorly and posteriorly to connect with adjacent bands (patterns 1 and 2, Fig. 13). The width of the bands varies from half a scale to 10 scales. In general, specimens from the Piedmont in Georgia, North Carolina, Virginia, and Maryland possess narrow bands (pattern 1, Fig. 13) whereas coastal specimens normally have bands 1.5 to 3 scales wide (pattern 2, Fig. 13). Specimens from the Apalachicola region in northern Florida occasionally have unusually wide bands of up to 10 scales (pattern 7, Fig. 13). The ventral pattern is highly variable, ranging from a generally light coloration suffused with dark (especially on the posterior margin of each scute) to a dark coloration with light areas. The juvenile pattern is identical with that of the adult (Fig. 12) except that occasional broods, especially from northern Florida and coastal Georgia, may consist of individuals with reddish yellow bands.

Discussion.—Two populations of *Lampropeltis getulus getulus* are recognizable on the basis of pattern and number of ventrals: a piedmont form with more numerous, narrower bands and a relatively higher number of ventrals, and a coastal form with fewer, wider bands and fewer ventrals. This distinction is valid for populations from New Jersey south to northern Georgia, but in

Figure 10. Distribution of *Lampropeltis getulus* in the United States and northern Mexico. Solid symbols represent localities of specimens examined, hollow symbols represent literature records. The *getulus* complex is represented by circles, the *splendida* complex by triangles, and the *californiae* complex by squares. Zones of intergradation within a complex are represented by shading, between subspecies complexes by crosshatching. A small triangle within another symbol represents a locality at which an intergrade between complexes has been found. Type localities are indicated by a star within a circle.

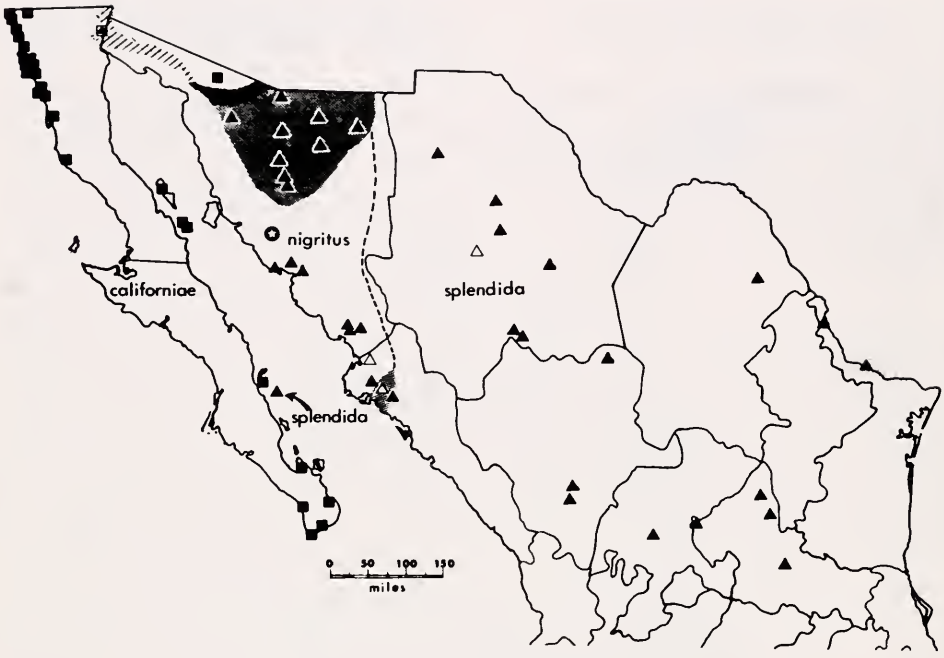


Figure 11. Distribution of *Lampropeltis getulus* in Mexico. For details of interpretation of symbols, see Figure 10.

southern Georgia and Alabama, and northern Florida, the number of ventrals is at the upper limits whereas the pattern is typical of the coastal form. I recognize these two populations as microgeographic races of *L.g. getulus*. Ecological and geographic separation apparently has enabled some degree of differentiation of these two groups, but the degree of differentiation does not warrant their subspecific recognition.

In portions of Florida (especially Wakulla, Leon, Jefferson, Taylor, Dixie and Levy counties) and in coastal Georgia (especially McIntosh County) specimens often possess light spotting between the dorsal bands (pattern 4, Fig. 13). This spotting may coalesce to form distinct bands, especially on the anterior third of the body. In central Florida, especially Alachua and Lake counties, specimens typically have a pattern of 23 to 52 (mean, 36.8) dorsal bands that normally do not fork (pattern 5, Fig. 13). I believe this pattern is the result of addition of bands in the manner described above. This spotting is the result of the influence of *L.g. floridana* as will be discussed below.

Lampropeltis getulus sticticeps Barbour and Engels and *L.g. goini* Neill and Allen are considered intergrades between *L.g. getulus* and *L.g. floridana*, and are discussed under *L.g. floridana*, below.

Lampropeltis getulus floridana Blanchard

Lampropeltis getulus floridana Blanchard, 1919: 1.
Lampropeltis getulus brooksi Barbour, 1919: 2.
Lampropeltis getulus sticticeps Barbour and Engels, 1942: 101.
Lampropeltis getulus goini Neill and Allen, 1949: 101.

Holotype.—USNM 22368 collected by William Palmer at Orange Hammock, DeSoto County (northeast portion), Florida.

Definition.—A subspecies of *L. getulus* characterized by 22 to 66 light crossbands (sometimes obscured) on a chocolate brown ground color that is ontogenetically reduced by basal lightening of each dorsal scale, 23 dorsal scale

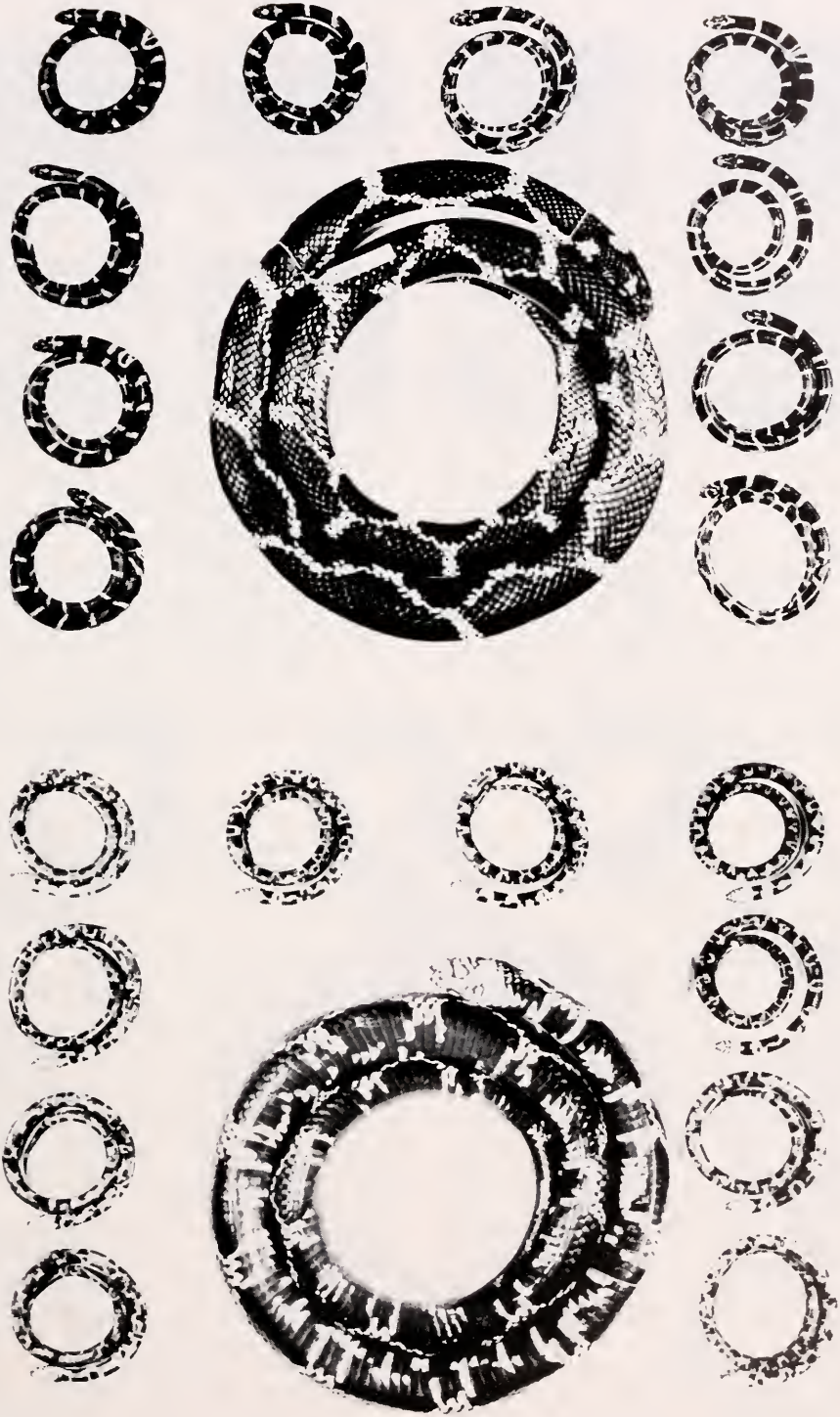


Figure 12. Adult and juvenile patterns of *Lampropeltis getulus getulus,* dorsum above and venter below (NCSM 5789, adult, and 5780-5799, brood, from Minnesota Beach, Pamlico County, North Carolina).

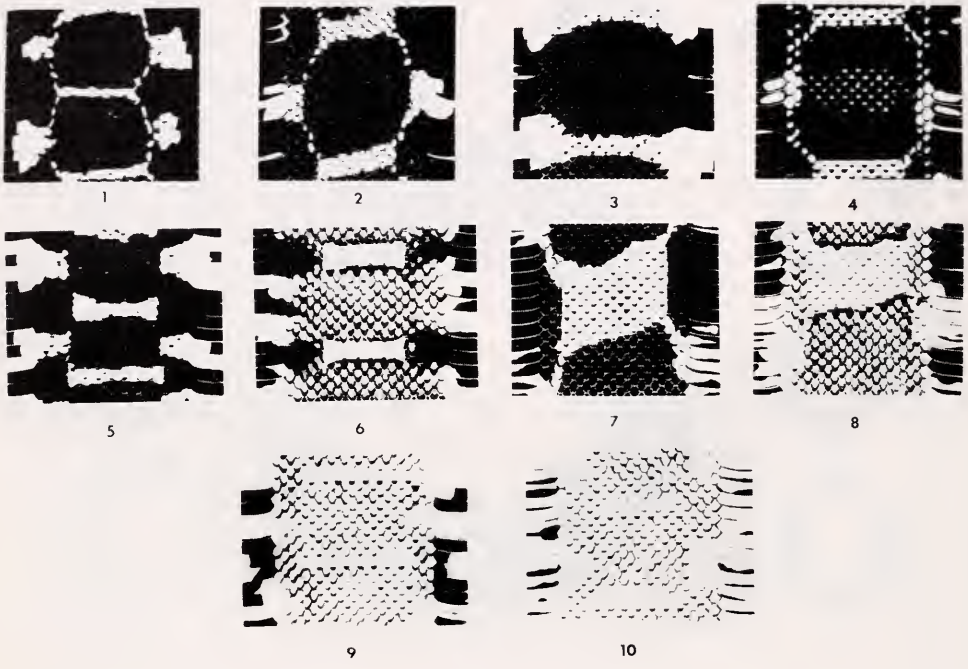


Figure 13. Basic pattern types of the *getulus* complex of *Lampropeltis getulus*. Patterns 1 through 5, *L.g. getulus*; patterns 6 through 8, intergrades between *L.g. getulus* and *L.g. floridana*; patterns 9 and 10, *L.g. floridana*.

rows, equal-sized genials, 1 + 2 or 2 intergenials, a higher than long loreal, and a deeply bilobed and laterally expanded hemipenis.

Range.—Southern Florida as far north as Pinellas and Hillsborough counties on the Gulf coast and southern and western Dade County on the Atlantic coast; a disjunct population in Duval and Baker counties in northeastern Florida.

Description.—Meristic and mensural data for this subspecies are as follows: ventrals 210 to 221 for both sexes; subcaudals 46 to 58 in males, 44 to 55 in females; infralabials usually 9 (85.1%), occasionally 10 (14.9%); loreal usually higher than long (57.9%) or slightly higher (15.8%), occasionally square (21.1%), rarely slightly longer (5.2%); intergenials usually 1 + 2 (86.2%), occasionally 2 (13.8%); anterior genials usually equal in length to the posterior genials (69.0%), occasionally slightly greater (13.8%), greater (6.9%), or smaller (10.3%); tail length 12.8% (10.9-14.3%) of the total length in males, 12.1% (10.2-13.8%) in females; snout length 31.3% (29.6-33.0%) of the head length in males, 30.7% (29.3-32.6%) in females.

The juvenile color pattern normally consists of yellow or reddish yellow crossbands on a brown ground color (Allen and Neill, 1954) (Fig. 14). As the individual matures, the scales in the dark areas between the bands develop light-colored spots on the basal portion of each scale until, in adults, only the posterior tip of each scale remains dark (pattern 9, Fig. 13). The dorsal bands may become almost completely obscured in some individuals (pattern 10, Fig. 13).

Discussion.—The concept of *L.g. floridana* has been severely modified since its original description by Blanchard (1919). Carr (1940), Conant (1958), and Carr and Goin (1959) have considered *L.g. floridana* to have pattern types similar to patterns 5 and 6 (Fig. 13). Their descriptions usually placed empha-

sis on the number of dorsal bands and light secondary spotting. This modification probably resulted from the recognition of *L.g. brooksi*, which was then distinguished by the differences in pattern. Carr and Goin (1959) characterized *L.g. brooksi* as "dull yellow, the scales being light in color and the dark ground color restricted to a small area on the tip of each scale. The pattern of bands is but slightly or not at all apparent."

Blanchard (1921) stated that *L.g. brooksi* "carries one step farther, and to its logical conclusion the interesting series of pattern changes of the *getulus* group in the southeast," thereby indicating the clinal relationship of the pattern types found from north to south on the Florida peninsula. Duellman and Schwartz (1958) placed *L.g. brooksi* Barbour in the synonymy of *L.g. floridana* Blanchard (which predates *brooksi* by one month) since both pattern types are found in "much of south-central Florida, as well as intermediate individuals over most of the range of *brooksi*." The results of this study support their conclusion.

Examination of the holotype of *L.g. brooksi* (MCZ 12456) revealed that this specimen has a pattern type identical with pattern 10 (Fig. 13). The dorsal bands, although somewhat obscure, are discernible. The pattern of the holotype of *L.g. floridana* is similar to pattern 9 (Fig. 13). The dorsal bands are more obvious as a result of the reduced secondary spotting. Both pattern types are, indeed, found throughout southern Florida and it is apparent that the differences are only a matter of slight degree.

The name *L.g. floridana* should be applied to the southern Florida population which has been considered *L.g. brooksi* by Carr (1940), Conant (1958), and Carr and Goin (1959). The central Florida populations, which typically have

Figure 14. Adult and juvenile pattern of *Lampropeltis getulus floridana* (NCSM 4455, adult, and 4707-4715, brood, from 6 miles S Monroe Station, Monroe County, Florida).

pattern 6 (Fig. 13), should be considered intergrades between *L.g. getulus* and *L.g. floridana*. These populations have been allocated to *L.g. floridana* by the authors noted above. For example, the specimen illustrating *L.g floridana* in the work by Carr and Goin (1959) is actually a specimen of *L.g. getulus* showing slight influence of *L.g. floridana* (pattern 5, Fig. 13).

The pattern of individuals from the zone of intergradation (Fig. 10) varies clinally from pattern 5 in the north with some secondary spotting between the bands (especially anteriorly) to pattern 6 in the south, showing an increase in the degree of secondary spotting. This pattern (6) is found farther south on the eastern coast than on the western coast. Specimens from around Lake Okeechobee (Highlands, Okeechobee, Martin, Palm Beach, Hendry, and Glades counties) are clearly intergrades. Specimens from as far south as Miami along the Miami oölite formation also show this pattern, and I consider them to be intergrades.

The populations of *L. getulus* from the Kissimmee Prairie in southwestern Osceola County, Florida, deserves special mention. This is an intergrade population consisting of individuals with patterns 5, 6, and 9. The area is probably close to the northeastern range limit of the southern Florida *L.g. floridana*.

These intergrade populations are also typically intermediate between *L.g. getulus* and *L.g. floridana* in the character of the number of dorsal scale rows. Fewer specimens possess a maximum of 23 scale rows toward the northern limits of the intergrade zone. However, even among samples of *L.g. getulus* from Alachua County, Florida, about half of the specimens examined possess 23 scale rows. This indicates influence from *L.g. floridana* since it is rare that a specimen of *L.g. getulus* from elsewhere in the range will have 23 dorsal scale rows.

The population of kingsnakes in extreme northeastern Florida (Baker and Duval counties) exhibit all the characters of *L.g. floridana*. Six specimens have been examined from Baker and western Duval counties which possess pattern types 9 or 10 (Fig. 13). For example, UF 2103 from 4 miles E Taylor, Baker County, or UF 3494 (Fig. 15) from between Marxville and Baldwin, Duval County, are indistinguishable from southern Florida populations, except in the number of dorsal bands (23 and 22, respectively, for the two specimens cited, while southern Florida populations average between 53 and 54). Specimens from eastern coastal Duval County and northern St. Johns County are typical *L.g. getulus* X *L.g. floridana* intergrades (pattern 6, Fig. 13), as for example, USNM 14140 from "Pilot town", Duval County, Florida. Since I have not seen any specimens which unquestionably originated from south of this area, I am not certain that the Duval and Baker county population is disjunct, but the evidence provided by intergrade specimens in the southeastern part of this range strongly suggests that this is the case. One specimen, however, USNM 64205 with data given as St. Johns Alligator Farm, St. Augustine, Florida, is allocated to *L.g. floridana*. The low number of dorsal bands (33) indicates that this specimen probably is related to the northeastern population. It is not possible to determine whether this specimen was collected at the Alligator Farm or was collected elsewhere and

Figure 15. ***Lampropeltis getulus floridana*** **(UF 3494 from Duval County, Florida).**

merely sent from the Alligator Farm to be deposited in the National Museum.

Specimens examined from populations immediately north of this apparently disjunct *L.g. floridana* population are primarily *L.g. getulus*. USNM 16698 from Fernandina, Nassau County, Florida, is a typically patterned *L.g. getulus* (pattern 2, Fig. 13) with a maximum of only 21 scale rows (19-21-19). Another specimen (LSUMZ 23509 from Amelia Island, Nassau County, Florida) with the same pattern shows indications of *L.g. floridana* influence in its dorsal scale reduction formula:

$$21 \frac{+6\ (46)}{+6\ (62)}\ 23 \frac{5\ +\ 6\ (127)}{5\ +\ 6\ (122)}$$

$$21 \frac{4\ +\ 5\ (204)}{4\ +\ 5\ (205)}\ 19\ [218].$$

Specimens from extreme southeastern Georgia are typical *L.g. getulus* with pattern 2 or 3 (Fig. 13). Populations on the offshore islands of McIntosh County, Georgia, however, are variable. UG 994 from Sapelo Island, McIntosh County, Georgia, has pattern 2 and is considered typical *L.g. getulus*, whereas UG 943 has pattern 4, the secondary spotting being most prominent between the anterior bands. In addition, the dorsal scale reduction is as follows:

$$21 \frac{+6\ (38)}{+6\ (49)}\ 23 \frac{4\ +\ 5\ (96)}{4\ +\ 5\ (105)}$$

$$21 \frac{3\ +\ 4\ (193)}{3\ +\ 4\ (187)}\ 19\ [209].$$

This specimen is therefore considered to be *L.g. getulus* with influence from *L.g. floridana*. Another specimen from the same locality (UG 944) has a pattern more typical of an intergrade (pattern 6, Fig. 13), but has a scale reduction similar to *L.g. getulus*:

$$21 \frac{4\ +\ 5\ (166)}{4\ +\ 5\ (161)}\ 19\ [210].$$

The entire population of Sapelo Island is therefore considered to be *L.g. getulus* with influence from *L.g. floridana*.

A specimen from 10 miles NE Fargo along the Suwannee River, Clinch County, Georgia (UG 400) is a typical intergrade between *L.g. getulus* and *L.g. floridana* (pattern 6, Fig. 13). This locality probably represents the northwestern limit of the zone of intergradation for the northeast Florida *L.g. floridana* population. However, three specimens (USNM 130143-130145) from the Okefenokee Swamp, Charlton Coun-

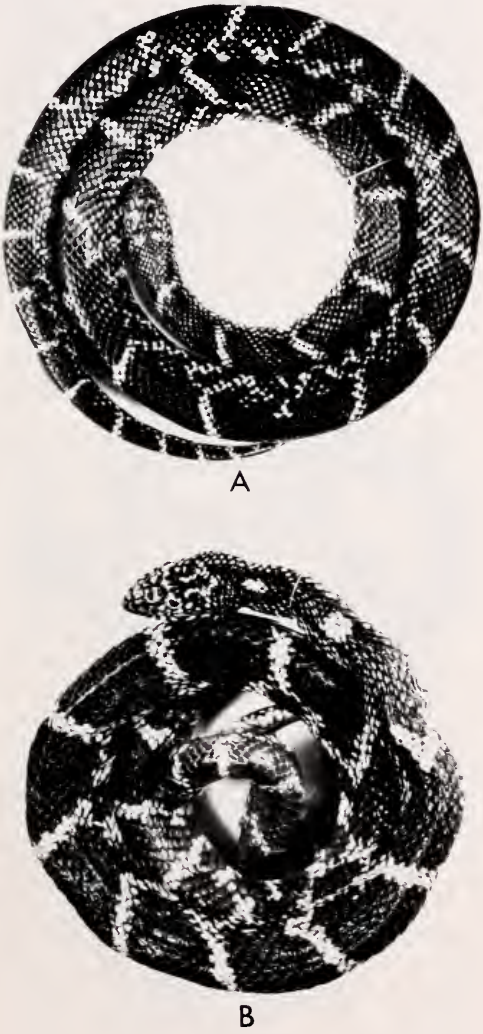


Figure 16. *Lampropeltis getulus* from the Outer Banks of North Carolina showing influence of *L.g. floridana* (A. NCSM 2020 from Hatteras, Dare County, North Carolina; B. MCZ 46469, holotype of *L.g. sticticeps*, from Ocracoke Island, Hyde County, North Carolina).

ty, Georgia, are typical *L.g. getulus*.

Barbour and Engels (1942) described a specimen (MCZ 46469) from Ocracoke Island, Hyde Couty, North Carolina, as a new subspecies, *L.g. sticticeps*, distinguishing it from *L.g. getulus* on the basis of "its broader and flatter head, heavily marked with white" and a pattern in which "the anterior rings appear in the form of spots, and the chain-like pattern does not begin until well down on the body, and from then on the familiar pattern is composed of white bands averaging two and one half to three times as broad as bands in the typical form." They further indicated a behavioral difference "so interesting that this fact alone would warrant its being named... for this snake, unlike all its allies, is not ophiophagous."

There is no question that this specimen is unusual. The head is aberrant in form, and the pattern is unusual for North Carolina. However, I have found spotting between the bands on several specimens from coastal North Carolina (*i.e.*, NCSM 3172 from 11 miles SW Bolton, Columbus County, and NCSM 2020 from Hatteras, Dare County). The holotype of *L.g. sticticeps* and the Hatteras specimen are shown in Fig. 16. There is also a difference in the number of ventral scutes between the specimens from the Outer Banks (200-207, mean 202.7 for 3 males; 204-207, mean 205.7 for 3 females) and the adjacent coastal mainland (206-216, mean 212.4 for 5 males; 205-210, mean 207.3 for 3 females). The Outer Banks population is therefore obviously not derived from the adjacent mainland. It is this difference in ventral count, plus the differences in pattern, head shape and rostrum length that prompted Lazell and Musick (1973) to argue that *L.g. sticticeps* should be considered valid. Their selected data did not consider either individual or geographic variation thereby negating their arguments. I will treat their remarks in detail in a separate paper. On the basis of the color pattern, which is similar to that of *L.g. getulus* X *L.g. floridana* intergrades, I suggest that this population was actually a relict population of *L.g. floridana* (a remnant of the ancestral type that gave rise to *L.g. getulus*) but is now an intergrade population. *L.g. sticticeps* Barbour and Engels should therefore be considered a junior synonym of *L.g. getulus* (Linnaeus) and *L.g. floridana* Blanchard.

Although *Lampropeltis getulus* is often ophiophagous, its diet is by no means restricted to snakes. These kingsnakes will eat any small mammal or bird in addition to reptiles (Clark, 1949; Hamilton and Pollack, 1956; Cunningham, 1959). I have found that individuals may have a preference for one type of prey or another depending on the habitat from which they came. In general, Florida specimens from swamp or marsh habitats tend to be more ophiophagous than specimens from dry areas. For example, several specimens that I collected from a farm near Lamont, Jefferson County, Florida, refused to eat snakes of any size or species, yet readily accepted birds and mammals. The method of killing the prey varied between constriction and the "*Coluber*-like habit" described by Barbour and Engels (1942).

Behavioral characteristics are probably inherited traits, but ones that may be considerably altered by environmental factors. This apparently is the case with the ophiophagous behavior of *L. getulus*. The dietary preferences of individuals may be inherently varied. Depending on the particular habitat, an individual may become habituated to a particular behavior, as for example, a preference for birds and mammals because of their relative abundance.

The kingsnakes in northwestern Florida from Gulf County east to southern Jefferson County differ considerably from neighboring populations. Individuals in that area may have a pattern of 15 to 18 dorsal crossbands, each 4 to 10 scales wide, on a brown ground color (pattern 7, Fig. 13; Fig. 17, C), or may be similarly patterned except that the dorsal scales between the bands are spotted (pattern 8, Fig. 13; Fig. 17, D). Specimens with this pattern formed the basis of the description of *L.g. goini* Neill and Allen (1949). I have, however, also examined speci-

mens from the same population which are typical *L.g. getulus* (Fig. 17, A) or typical *L.g. floridana* (Fig. 17, D). Even specimens from the type locality of *L.g. goini* (Wewahitchka, Gulf County, Florida) may have a pattern more typical of *L.g. getulus* (Fig. 17, B). In addition, several specimens possess a maximum of 23 dorsal scale rows, typical of *L.g. floridana*.

This population, therefore, consists of *L.g. getulus, L.g. floridana*, intermediate specimens, and broad-banded individuals (the significance of which is discussed in the conclusions section below), and is consequently considered to be an intergrade population. The name *L.g. goini* Neill and Allen is therefore placed in the synonymy of *L.g. getulus* (Linnaeus) and *L.g. floridana* Blanchard.

THE *SPLENDIDA* COMPLEX

The *Splendida* Complex

Lampropeltis getulus holbrooki Stejneger

Coronella sayi: Holbrooki, 1842: 99.
Ophibolus getulus sayi: Cope, 1875: 37.
Ophibolus getulus getulus: Cope, 1880: 23.
Lampropeltis holbrooki Stejneger, 1903: 152. Substitute name.
Lampropeltis getulua holbrooki: Bailey, 1905: 47.
Lampropeltis getulus holbrooki: Hurter and Strecker, 1909: 26.
Lampropeltis getulus holbrookii: Strecker, 1909: 7.

Holotype.—None designated. In a footnote, Stejneger (1903) proposed the name *Lampropeltis holbrooki* as a substitute name for Holbrook's (1842) *Coronella sayi*, a misapplication of *Coluber sayi* Schlegel, 1837 (= *Pituophis*

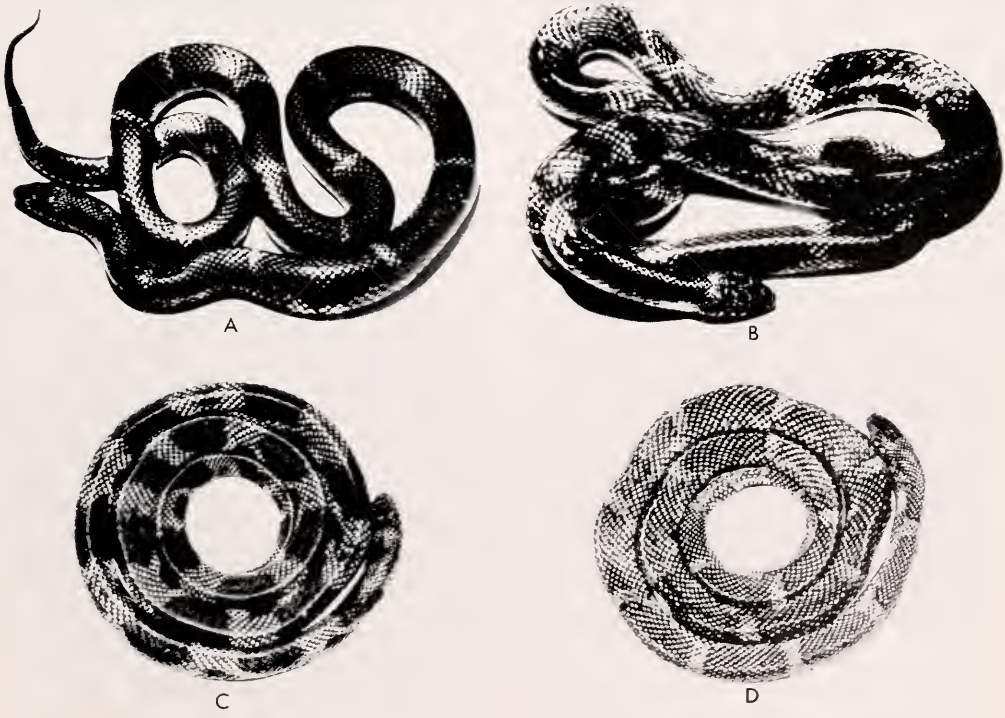


Figure 17. *Lampropeltis getulus* from the Apalachicola River region, Florida: A.N Apalachicola, Gulf County, Florida (specimen not available); B.E. Wewahitchka, Gulf County, Florida (specimen not available); C. LSUMZ 23511 from 6 miles E Wacissa, Jefferson County, Florida; D. LSUMZ 23510 from 3 miles N Carabelle, Franklin County, Florida.

melanoleucus sayi). Stejneger (1903) did not indicate any type locality, but Stejneger and Barbour (1917) gave it as "valley of the Mississippi."

Definition.—A subspecies of *L. getulus* characterized by a dark brown or black ground color with most or all of the dorsal scales having a central light-colored spot, 21 dorsal scale rows, anterior genials equal to or longer than posterior genials, 1 + 2 intergenials, a square loreal, and a slightly bilobed hemipenis.

Range.—Southern Iowa and western Illinois south to eastern Texas, Louisiana, most of Mississippi, and central and southwestern Alabama.

Description.—Ventrals 197 to 221 in males, 198 to 222 in females; subcaudals 46 to 59 in males, 37 to 51 in females; infralabials usually 9 (84.2%), occasionally 10 (14.8%), rarely 8 (0.7%) or 11 (0.3%); loreal square (53.5%), slightly higher than long (12.3%), or slightly longer than high (8.6%), occasionally longer (11.1%) or higher (12.5%); intergenials normally 1 + 2 (83.1%), sometimes 2 + 2 (6.6%) or 2 (7.3%), rarely 2 + 3 (0.3%), 1 (1.3%), or 1 + 1 (1.4%); anterior genials often longer than posterior genials (48.8%), sometimes equal (30.0%), occasionally slightly greater (19.0%), rarely shorter (2.2%); tail length 13.2% (11.0-15.3%) of total length in males, 12.3% (10.1-14.5%) in females; snout length 30.4% (27.7-34.0%) of head length in males, 30.8% (28.4-34.2%) in females.

The pattern of *L.g. holbrooki* includes several different types. In Missouri, western Arkansas, eastern Oklahoma, eastern Texas, and a portion of southwestern Louisiana (excluding the coastal marsh), specimens exhibit pattern 11 (Fig. 22). Each scale of the dorsum has a centrally located, small, round spot. On the first two or three scale rows, however, the spots are larger, leaving only the edges of each scale dark. The ventral pattern may be either uniformly light with the posterior edge of each scute dark, or it may have regular squarish blotches. The ventral side of the tail is light except for the posterior margin of each subcaudal scale. In life the ground color is normally black with pale or bright yellow spotting.

Specimens from the Mississippi River valley from southern Iowa and western Illinois southward to Louisiana possess a very different pattern. The cream or yellow spots in each scale are irregular in shape, and some of the dorsal spots are expanded laterally to form 39 to 94 irregular dorsal bands (pattern 15, Fig. 22). The venter is extremely variable and may range from predominantly light to predominantly dark (Fig. 18). About one-third of the specimens examined from the Louisiana coastal marshes have a red or reddish yellow ventral color.

The pattern found in specimens from eastern Mississippi and western Alabama is more regular than the Mississippi River bottomland type in that the spots are generally symmetrical, although some of the dorsal scales contain spots expanded laterally to form indistinct dorsal bands (pattern 13, Fig. 22).

Intermediate pattern types between the above basic patterns are discussed below.

The juvenile pattern consists of distinct dorsal bands with little or no spotting between the bands, and some spotting on the lateral scale rows (Fig. 19). The spots on the dorsal scales develop with the growth of the individual. Occasional adults have been found which retain the juvenile pattern (Fig. 20, D).

Discussion.—The geographic distribution of pattern types 11, 13, and 15 is shown in Fig. 21. The marked differentiation within *L.g. holbrooki* enables the recognition of three distinct subdivisions that I regard as microgeographic races of *L.g. holbrooki*. Populations intermediate in pattern type have been found between each of these microgeographic races. For example, the Louisiana specimen shown in Fig. 20, A, is typical of the southern populations of the uniformly spotted form (pattern 11), and the kingsnake shown in Fig. 20, C, is typical of the Mississippi bottomland populations (pattern 15). Intermediate specimens (Fig. 20, B) are similar to the spotted form in that the spots are more

regular, but some of the spots on the dorsal scales are elongated and oriented laterally forming dorsal bands (pattern 12, Fig. 22). The light spots on the first two or three scale rows are also enlarged so that each scale in these rows may be described as yellow with a dark edge. The kingsnake described by Holbrook (1842) as *Coronella sayi* Schlegel was such an intermediate specimen. Based on his description of pattern, and the number of ventrals and subcaudals, it is probable that Holbrook's specimen from which his figure 22 was drawn, was from

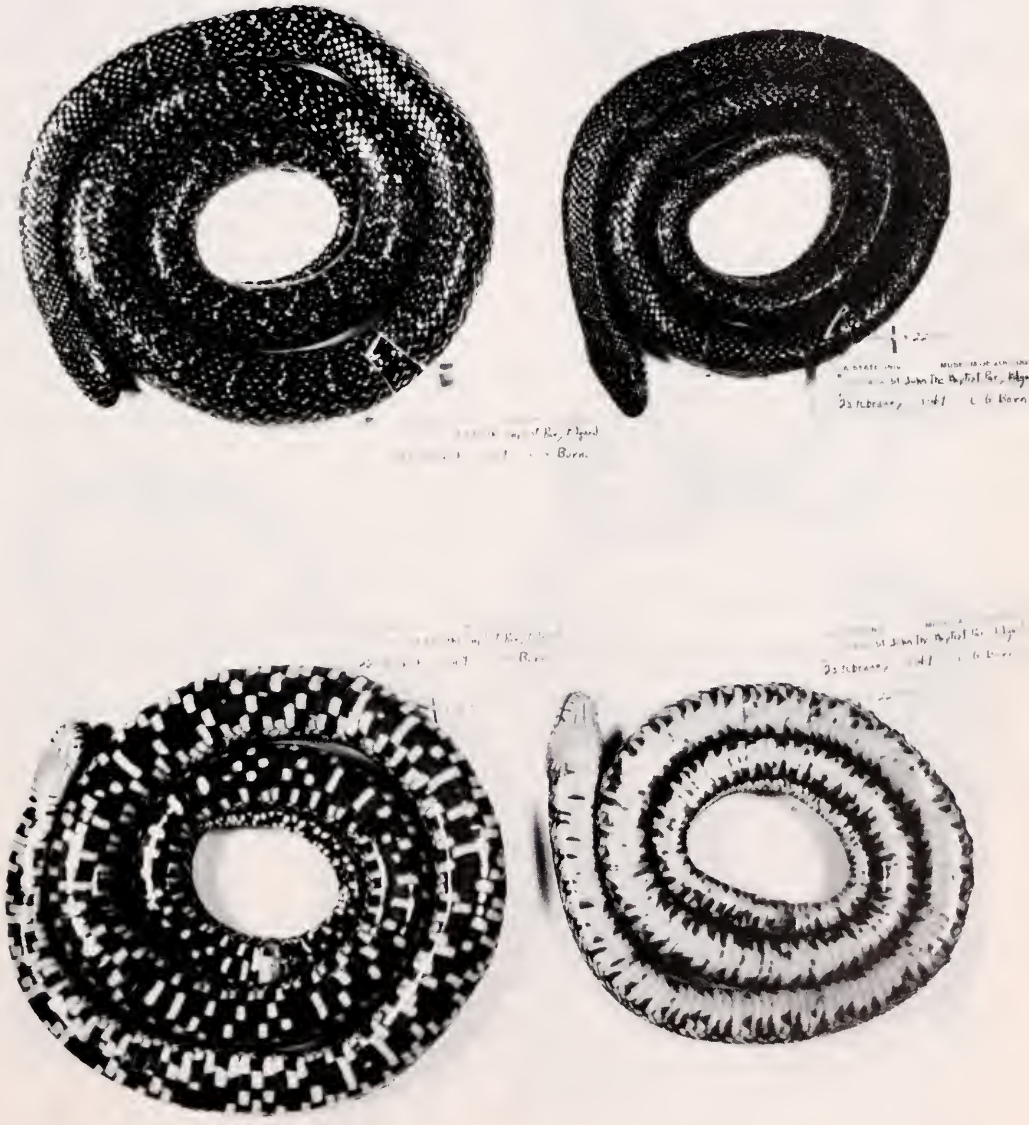


Figure 18. Variation in ventral pattern of *Lampropeltis getulus holbrooki* (Left, dorsum and venter, LSUMZ 22054, right dorsum and venter, LSUMZ 22055, both from Edgard, St. John the Baptist Parish, Louisiana).

Figure 19. Juveniles of *Lampropeltis getulus holbrooki* (A. LSUMZ 19006 from 0.5 miles NW Kraemer, LaFourche Parish, Louisiana; B. LSUMZ 19336 from Mobile Bay, Baldwin County, Alabama).

central or northeastern Arkansas, certainly not from the Mississippi bottomlands as suggested by Stejneger and Barbour (1917) when they restricted the type locality to the "valley of the Mississippi." The specimen shown by Anderson (1965: 244 B) is also intermediate in pattern, but the *L.g. holbrooki* illustrated by P.W. Smith (1961: 216) is clearly the western form (pattern 11).

Although the three microgeographic races are readily distinguishable, I do not regard their level of differentiation as sufficient to elevate them to subspecific rank. Their degree of differentiation is less than is evident between any other subspecies in the *splendida* complex.

Intergradation between *L.g. holbrooki* and *L.g. niger*, and between *L.g. holbrooki* and *L.g. getulus* is discussed under *L.g. niger*.

Lampropeltis getulus niger (Yarrow)

Ophibolus getulus niger Yarrow, 1882: 438.
Ophibolus getulus sayi: Blatchley, 1891: 32.
Lampropeltis getulus niger: Blanchard, 1920: 2.
Lampropeltis getulus nigra: Pratt, 1923: 221.

Cotypes.—USNM 12149 (2 specimens) collected by Robert Ridgway at Wheatland, Knox County, Indiana.

Definition.—A subspecies of *L. getulus* characterized by a black ground color often with some dorsal scales marked with small light spots to form 21 to 70 dorsal bands, a maximum of 21 dorsal scale rows, anterior genials equal to or longer than posterior genials, 1 + 2 intergenials, a square loreal, and a slightly bilobed hemipenis.

Range.—Eastern Illinois, southern Indiana, extreme central southern Ohio, western West Virginia, Kentucky, eastern two-thirds of Tennessee, northwestern Georgia, and northeastern Alabama.

Description.—Ventrals 198 to 217 in males, 198 to 216 in females; subcaudals 45 to 55 in males, 39 to 51 in females; infralabials usually 9 (82.3%), occasionally 10 (12.3%), rarely 8 (4.6%) or 11 (0.8%); loreal usually square (50.9%), slightly higher than long (11.6%) or higher than long (17.0%), sometimes longer (11.6%) or slightly longer (3.6%); intergenials normally 1 + 2 (78.0%), occasionally 2 (18.1%), rarely 2 + 2 (2.4%) or 1 (1.5%); anterior genials usually equal to posterior genials (42.6%), slightly greater (20.9%) or greater (32.2%), rarely shorter (4.3%); tail length 13.0% (10.8-14.6%) of total length in males, 12.2% (10.0-13.7%) in females; snout length 30.2% (27.0-32.3%) of head length in males, 31.1% (29.4-33.6%) in females.

The dorsal pattern is essentially a reduced juvenile pattern of *L.g. holbrooki*. Juvenile *L.g. niger* (Fig. 23) have a pattern similar to *L.g. holbrooki*, but usually with fewer bands. As the

individual matures, this pattern becomes reduced. The adult pattern may retain the dorsal bands only as a series of spots (pattern 17, Fig. 22), or they may be so reduced as to be almost indiscernible (pattern 18, Fig. 22).

Discussion.—Blanchard (1921) recognized that the pattern of *L.g. niger* is simply a reduction of the *L.g. holbrooki* juvenile pattern. He believed *L.g. niger* to be a valid subspecies, but indicated the possibility that it might be only a "local or inconsistent variation of *holbrooki*." The results of my study confirm that *L.g. niger* is a valid subspecies readily identified by its pattern. Although occasional specimens of *L.g. holbrooki* may be similar in pattern to *L.g. niger* through retention of the juvenile pattern (Fig. 20, D), no specimens were found within the defined range of *L.g. niger* that had developed secondary spotting similar to that of *L.g. holbrooki* (Fig. 24). Specimens from the periphery of the range, however, develop spotting laterally and dorsally and are considered intergrades between *L.g. niger* and *L.g. holbrooki* (pattern 16, Fig. 22).

P.W. Smith (1961) stated that intergradation between *L.g. holbrooki* and *L.g. niger* in Illinois "is exhibited by specimens from extreme southwestern Illinois, and intergrades probably occur in most of the southern Division." Specimens from Coles, Cumberland, Jasper, and Richland counties, Illinois, are typical *L.g. niger* whereas Shelby and Effingham county specimens have pattern 16 (Fig. 22) and are considered intergrades. A specimen (UIMNH 50818) from 4 miles SE Carlinville, McCoupin County, Illinois, is intermediate between patterns 12 and 16, and is considered *L.g. holbrooki* with *L.g. niger* influence. This probably represents the northwestern limit of the zone of intergradation. However, another specimen (INHS 3031) from 4 miles N Old Ripley, Bond County,

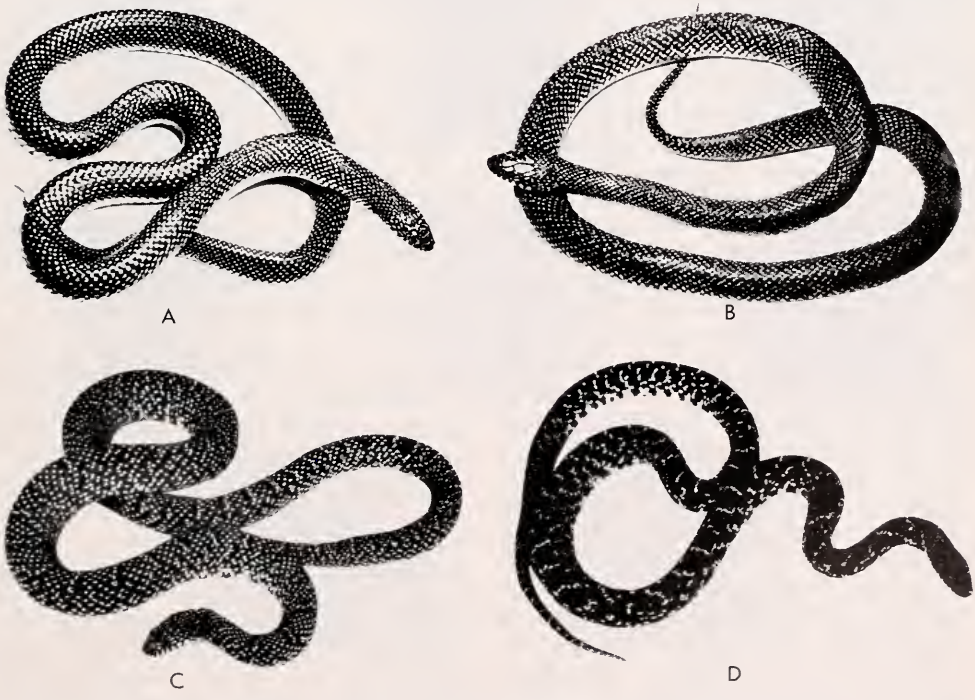


Figure 20. Pattern variation in *Lampropeltis getulus holbrooki* (A. LSUMZ 23508 from 2 miles S Holmwood, Calcasieu Parish, Louisiana; B. RAT uncatalogued specimen from Lafayette, Lafayette Parish, Louisiana; C. and D. LSUMZ 19004 and 19007 from 0.5 miles NW Kraemer, LaFourche Parish, Louisiana).

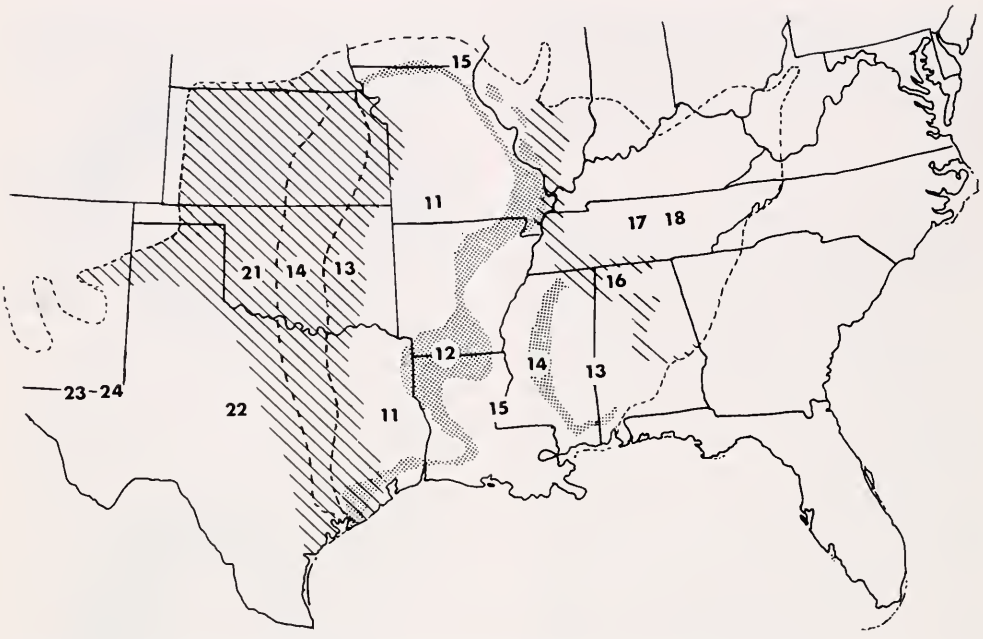


Figure 21. The geographic distribution of pattern types in the *splendida* complex of *Lampropeltis getulus*. Numbers refer to pattern types in Figures 22 and 31.

Illinois, (southeast of the McCoupin County record) is typical of *L.g. holbrooki* (pattern 11). The entire population in southern Illinois (southeast of Randolph County), extreme western Kentucky (Trigg County westward), and northwestern Tennessee consists of intergrades. The specimen labled *L.g. niger* by P.W. Smith (1961: 217) is an intergrade between *L.g. niger* and *L.g. holbrooki*.

Specimens from southern Tennessee from Franklin County westward are also intergrades between *L.g. niger* and *L.g. holbrooki*. MSU 1545 from 2 miles NW Myrtle, Union County, Mississippi, has a reduced *L.g. holbrooki* pattern with very small spots between the dorsal bands and small lateral spots, thereby showing influence of *L.g. niger*. This locality marks the northeastern limit of *L.g. holbrooki* in Mississippi. The zone of intergradation in central Alabama is evidenced by intermediate specimens (pattern 16, Fig. 22) from St. Clair, Jefferson, Shelby, Chilton, and Elmore counties. The insufficient number of specimens from northern Alabama does not permit an accurate analysis of the zone of intergradation in this area. Two specimens from Colbert County (USNM 51217 from Leighton and USNM 2319 from Tuscumbia), however, are typical of *L.g. niger*. USNM 51217 shows a slight tendency toward pattern 16. A specimen (UAHC 52-1077) from Smither's Mountain, near Huntsville, Madison County, is clearly an intergrade (Fig. 25).

Relationships with The *Getulus* Complex

Typical adult *L.g. niger* may have a completely dark dorsum with only slight traces of the juvenile crossbands, which are represented by a series of light spots (Fig. 24, A and B). The degree of ontogenetic pattern reduction varies individually, not geographically. Adult specimens often retain distinct dorsal bands (Fig. 24, C). Occasional adult specimens may retain the broad juvenile bands, as for example, LSUMZ 19015 (Fig. 24, D), a male with a total length of 1100 mm. Such specimens are distinguished from *L.g. getulus* by the bands, which are always composed of a series of

Figure 23. Juvenile pattern of *Lampropeltis getulus niger* (from 12.5 air miles SSE Benton, Polk County, Tennessee; specimen not available).

spots rather than continuous as in the latter form.

Blanchard (1921) emphasized the number of dorsal bands as a criterion in *getulus*, but their number is 38 and 31 [body + tail bands], respectively, and one would doubtless not hesitate to assign them to *getulus*." The Augusta specimen (USNM 8797) is a female *L.g. niger* (pattern 17) with only 24 dorsal bands and 209 ventrals. The reduced number of bands results from loss of bands by extreme darkening. However, all other specimens from this area to northeastern Georgia are typical of *L.g. getulus*. Furthermore, the number of ventrals is a little low for this area (mean 215.1, range 210 to 220, for females). The locality data, therefore, are doubtful. USNM 9109 from Marietta, Cobb County, distinguishing *L.g. niger* from *L.g. getulus*. He cited a specimen of *L.g. getulus* from the Cherokee Nation, North Carolina (USNM 15291), with 37 crossbands (30 on the body) which "presents a strong contrast with one [*L.g. niger*] from

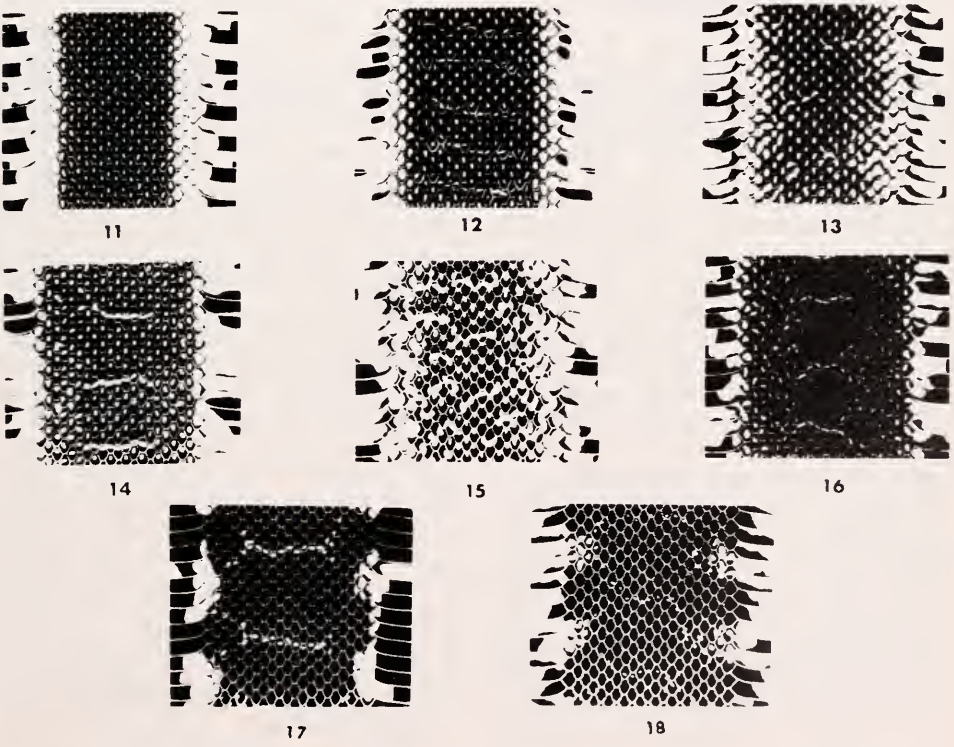


Figure 22. Basic pattern types of the eastern representatives of the *splendida* complex of *Lampropeltis getulus*. Patterns 11 through 15, *L.g. holbrooki*; pattern 16, intergrade between *L.g. holbrooki* and *L.g. niger*; pattern 17 and 18, *L.g. niger*.

Figure 24. Pattern variation in *Lampropeltis getulus niger* (A. and B. LSUMZ 19027 and 19028 from the Chatahoochee National Forest, 14 air miles NNE Chatsworth, Murray County, Georgia; C. LSUMZ 19012 from Dentville, McMinn County, Tennessee; D. LSUMZ 19015 from the Cherokee National Forest, 12.5 miles SSE Benton, Polk County, Tennessee).

so short a distance west as Knoxville, Tennessee, with 73." I have found a great amount of variation in dorsal band number in *L.g. niger*. In eastern Tennessee, for example, the average number of body bands, when present, is 40.1, but the number varies from 21 to 61.

Blanchard (1921) further stated that *L.g. getulus* and *L.g. niger* "might be supposed to be distinct even where their ranges meet, but specimens from Georgia and Alabama practically prove intergradation. The specimens from Marietta and from Augusta, Georgia, cited by Yarrow (1882: 91), have the cross bands very narrow, unlike any typical Georgia, is also typical *L.g. niger* (pattern 17). This female has 30 dorsal bands and 203 ventrals which is within the limits of the *L.g. niger* populations in northwestern Georgia. Another specimen (UIMNH 18625), a male from 4 miles S Hapeville, Clayton County, Georgia, is typical of *L.g. getulus* (pattern 1) with 21 dorsal bands and 215 ventrals. Data for this animal agree with adjacent *L.g. getulus* populations. The distance between these two localities is only about 20 miles.

A third specimen (UIMNH 35739), a male from Atlanta, Fulton County, midway between the above two localities, is intermediate in pattern (pattern 19, Fig. 26) and has 207 ventrals and 19 dorsal bands. I consider this specimen to be an intergrade between *L.g. getulus* and *L.g. niger*.

The occurrence of intergradation between members of the *splendida* complex (both *L.g. niger* and *L.g. holbrooki*) and *L.g. getulus* is rare. In addition to the above mentioned specimen, I have seen intergrades between *L.g. niger* and *L.g. getulus* in Lee County, Alabama. King (1939) reported another specimen (unavailable) from Deals Gap at the southwestern end of the Great Smoky Mountains National Park as

"a perfect intergrade between *L.g. getulus* and *L.g. nigra*."

In Lee County, Alabama, *L.g. niger* and *L.g. getulus* are sympatric at least from 10 miles south to 9 miles north of Auburn, and west to Loachapoka. The two subspecies are again readily distinguishable on the basis of pattern with the bands of *L.g. niger* consisting of a series of spots and the bands of *L.g. getulus* being continuous (Fig. 27). Specimens of *L.g. getulus* also tend to have a higher number of ventrals: 215 (210-220) for *getulus*, 212.2 (210-216) for *niger*, and 210.7 (207-212) for intermediates. In this area, *L.g. getulus* is apparently the common form, since 8 of the 16 specimens examined (AU collections) are of this subspecies, 4 are *L.g. niger*, and 4 are intermediate. I do not know whether there is ecological separation in this area. AU 34 from Dowdells Swamp, 10 miles SW Auburn, is typical of *L.g. niger* (pattern 17), while AU 890 with locality data given only as 10 miles SW Auburn, is typical of *L.g. getulus* (pattern 1). AU 429 from 10 miles SW Auburn is intermediate (Fig. 28).

In addition to the pattern, the distinctiveness of the hemipenial form is diagnostic. Members of the *getulus* complex have hemipenes that are expanded at the distal end, while the hemipenes in the *splendida* complex are not expanded. The everted hemipenes of all of the intergrade specimens are intermediate in hemipenial form (Fig. 29).

Available specimens intermediate between *L.g. holbrooki* and *L.g. getulus* are equally rare: AU 9118 from 3.9 miles S Georgiana, Butler County, Alabama; AU 6246 from Holy Mill Creek, 3 miles W Blacksher, Baldwin County, Alabama; AU 8859 from Perkins Landing on the Tensaw River, 8.6 air miles WSW Bay Minette, Baldwin County, Alabama; AU 8996 from the Baldwin—Mobile County line, Mobile Bay Causeway (US 90). The pattern of *L.g. getulus* and *L.g. holbrooki* intergrades consists of wide, distinct bands across the central 8 to 12 scale rows with some secondary spotting between the bands and on the lateral scales (pattern 20, Fig. 26). The hemipenis of one of the two males is everted and is also intermediate in form (Fig. 29).

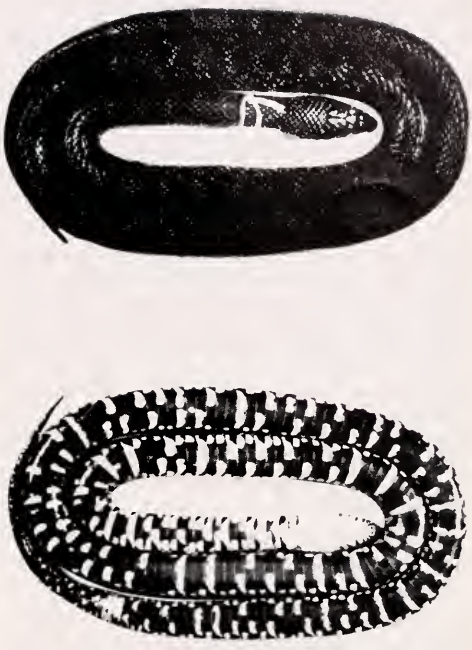


Figure 25. Intergrade between *Lampropeltis getulus holbrooki* and *L.g. niger* (UAHC 52-1077 from Smither's Mountain, Madison County, Alabama).

Another Monroe County specimen (AU 2964) from Hybart (9 miles N Holly Mill Creek) is typical of *L.g. holbrooki* with 45 dorsal bands (compared with 27 for AU 6246) and 218 ventrals (compared to 208 for AU 6246, both females).

Additional locality records for Baldwin County are as follows: *L.g. getulus*—Silver Hill (MCZ 47885); 3 miles S US 31 on Alabama 112, east of Bay Minette (Yancy Junior College, Bay Minette, uncatalogued specimen); Midway on Morgan Peninsula (AU 3830); *L.g. holbrooki*—0.8 miles E Apalachee River, US 90, Mobile Bay (LSUMZ 19336); 1.0 mile E Apalachee River, US 90, Mobile Bay (LSUMZ 19010).

The distribution of *L.g. getulus, L.g. niger,* and *L.g. holbrooki* strongly indicates that there is a narrow zone of

contact between *L.g. getulus* and *L.g. niger*, and *L.g. getulus* and *L.g. holbrooki*, with only occasional interbreeding. This phenomenon suggests that *L.g. getulus* is not derived from either *L.g. niger* or *L.g. holbrooki*.

Lampropeltis getulus splendida (Baird and Girard)

Ophibolus splendida Baird and Girard, 1853: 83.
Ophibolus sayi: Baird and Girard, 1853: 159.
Ophibolus getulus splendidus: Cope, 1875: 37.
Ophibolus getulus sayi: Brown, 1901: 77.
Lampropeltis getulus splendidus: Wright and Bishop, 1915: 148.
Lampropeltis getulus splendida: Blanchard, 1920: 2.
Lampropeltis catalinensis Van Denburgh and Slevin, 1921: 397.
Lampropeltis getulus catalinensis: Soule and Sloan, 1966: 142.

Holotype.—USNM 1726 collected by Col. J.D. Graham in Sonora, Mexico.

Definition.—A subspecies of *L. getulus* characterized by a dark brown or black ground color with each of the lateral scales having a central light-colored spot and occasional light scales in the medial scale rows forming 42 to 97 crossbands, 23 or 25 dorsal scale rows, anterior genials usually much longer than posterior genials, usually 2 + 2 intergenials, a square or longer than high loreal, and a moderately bilobed hemipenis.

Range.—Central Texas west to southeastern Arizona and southward to San Luis Potosi and Zacatecas, Mexico, and Santa Catalina Island, Gulf of California, Mexico.

Description.—Ventrals 199 to 227 in males, 203 to 237 in females; subcaudals 45 to 62 in males, 40 to 52 in females; infralabials usually 9 (83.0%), occasionally 10 (17.0%); loreal square (38.4%), slightly longer than high (22.6%) or longer than high (22.1%), rarely higher than long (9.5%) or slightly higher than long (7.4%); intergenials normally 2 + 2 (62.0%), often 2 + 3 (22.2%) especially in the western portion of the range, occasionally 1 + 2 (10.9%) in the eastern part of the range, rarely 2 (4.6%) or 1 + 1 (1.0%); anterior genials usually much longer than the posterior genials (62.8%), or slightly longer (21.0%), occasionally equal (16.2%); tail length

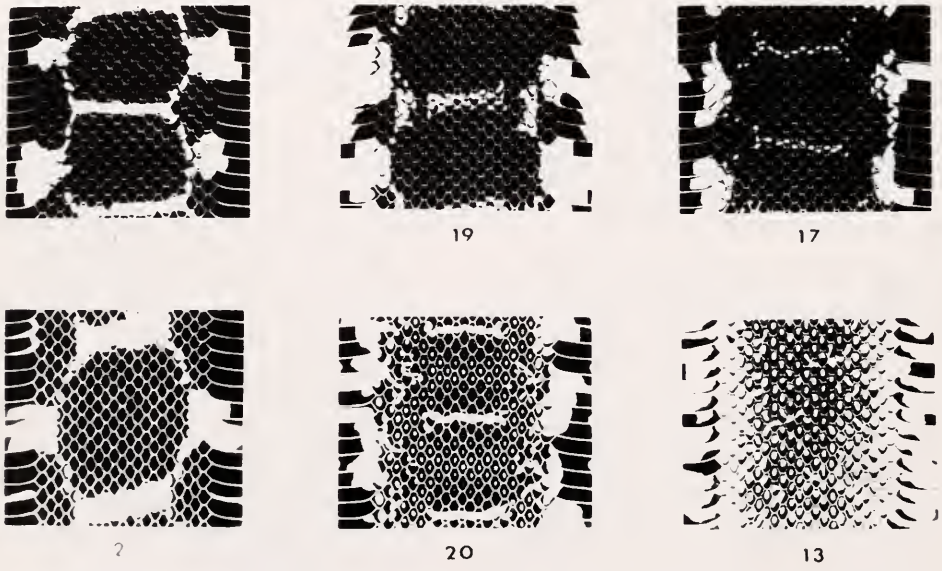


Figure 26. Pattern types of intergrades between *Lampropeltis g. getulus* and the eastern members of the *splendida* complex (*L.g. holbrooki* and *L.g. niger*). Patterns 1 and 2, *L.g. getulus*; pattern 19, intergrade between *L.g. getulus* and *L.g. niger*; pattern 20, intergrade between *L.g. getulus* and *L.g. holbrooki*; pattern 17, *L.g. niger*; pattern 13, *L.g. holbrooki*.

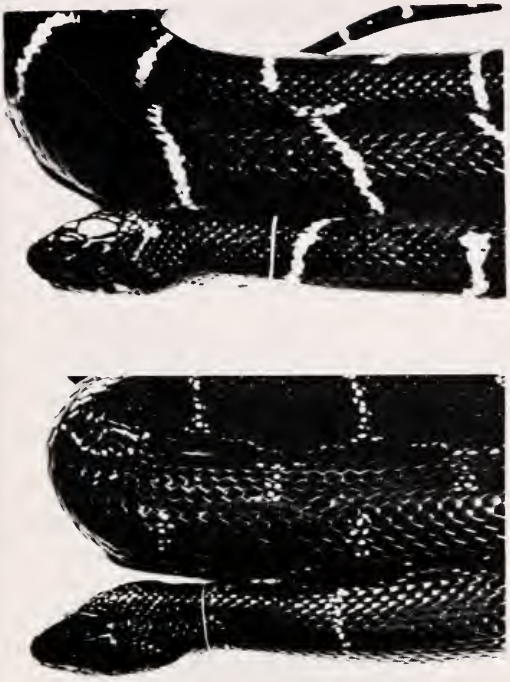


Figure 27. Specimens from the area of sympatry for *Lampropeltis g. getulus* and *L.g. niger* (Top, *L.g. getulus*, AU 416 from 5 miles S Auburn, Lee County, Alabama; bottom, *L.g. niger*, AU 35, from 4.5 miles NW Loachipoka, Lee County, Alabama).

13.4% (10.9-14.1%) of total length in males, 12.4% (11.3-13.5%) in females; snout length 30.5% (27.9-32.2%) of head length in males, 31.2% (29.4-33.2%) in females.

The pattern usually is as illustrated in Fig. 31, pattern 23, with yellow or cream spotting. The venter is usually dark except for the light anal plate. Dorsal bands may consist of a series of spots, may be broad (to two scales wide), or may be absent. Occasional specimens may be completely spotted with the dorsal scales each containing a centrally located light-colored spot, although these spots are usually smaller than the lateral spots (pattern 24, Fig. 31). Specimens from the eastern limits of the range often have an irregular pattern with a blotched rather than a uniform venter (pattern 22, Fig. 31). Juvenile patterns do not differ from that of the adult.

Discussion.—Van Denburgh and Sleven (1921) described *Lampropeltis catalinensis* from Santa Catalina Island, Gulf of California, on the basis of a single adult male (CAS 50514) "which was dug out from the center of a decayed fallen cactus" (Van Denburgh, 1922). Van Denburgh and Slevin (1921) described the pattern as follows: "no transverse markings, a dark purplish brown longitudinal dorsal band about five scales wide from head to end of tail. All lateral scales yellowish white with narrow purplish brown borders. Along the middorsal line, at nearly regular intervals of three or four scales, are small yellowish white spots on single scales. Head dark brown above and laterally, with small yellowish white markings on internasals, prefrontals, temporals, oculars, loreal, nasals, rostral, and labials. Lower surfaces chiefly black, marbled with yellowish

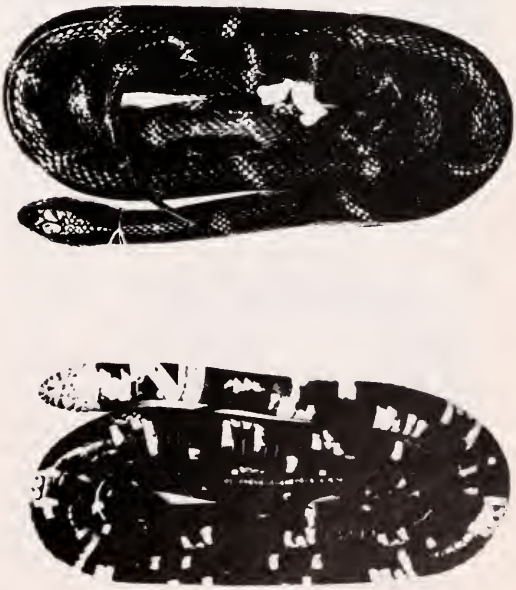


Figure 28. An intergrade between *Lampropeltis g. getulus* and *L.g. niger* (dorsum and venter of AU 429 from 10 miles SW Auburn, Lee County, Alabama).

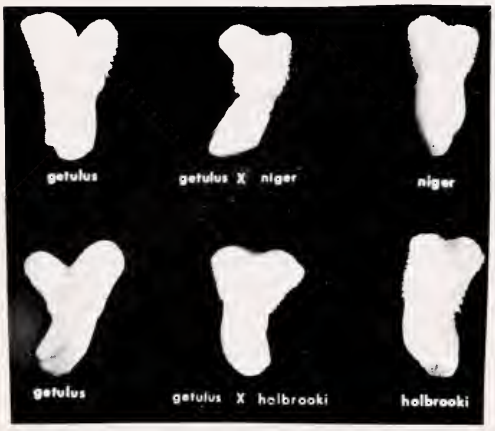


Figure 29. Hemipenes of intergrades between members of the *getulus* complex and the *splendida* complex of *Lampropeltis getulus*. Top row—*L.g. getulus*, NCSM 5175 from 4¾ miles NW Laurel Hill, Scotland County, North Carolina;*L.g. getulus* X *L.g. niger*, AU 429 from 10 miles SW Auburn, Lee County, Alabama; *L.g. niger*, UF 10775 from Euchee Focks, Meigs County, Tennessee. Bottom row—*L.g. getulus*, UF 2998 from 4 miles E Thomasville, Thomas County, Georgia; *L.g. getulus* X *L.g. holbrooki*, AU 9159 from 1.5 air miles W Blecksher, Baldwin County, Alabama; *L.g. holbrooki*, MSU 1639 from the west end of Horn Island, Jackson County, Mississippi.

white laterally on most of the gastrosteges, and centrally on a few; the distal urosteges and the genials and gulars yellowish white with black or brown margins." Van Denburgh (1922) added that "the ground color above is dark purplish brown, similar to that of some specimens of *L. californiae*." This purplish brown coloration is the same as the chocolate brown that I have used to describe the lighter colored specimens. Van Denburgh (1922) further stated that the coloration "is quite different from any other known species, although the lower surfaces are somewhat suggestive of *L. nitida* and the spotted sides remind one of *L.g. splendida*."

Cliff (1954) shortened the description of the coloration to "a purple longitudinal dorsal band..." and stated that "the only other *Lampropeltis* with a color pattern near that of *catalinensis* is *L. nitida* from the Cape region of Baja, California."

The following data were obtained from the holotype (CAS 50514): ventrals 226; subcaudals 62; supralabials 8, fourth and fifth entering the orbit; infralabials 10/9; temporals 2 + 4/2 + 3; oculars 1 + 2; anterior genials much longer than posterior; intergenials 2 + 3; dorsal scale reduction $23\ \frac{4+5\ (147)}{6+7\ (138)}\ 21\ \frac{3+4\ (183)}{3+4\ (190)}\ 19$; length 984 + 157 mm; pattern type 23 with 68 narrow crossbands consisting of a series of light spots.

The pattern of *L. catalinensis* is identical in all respects with that typical of *L.g. splendida* (Fig. 30). In addition, the holotype of *L. catalinensis* agrees in all other characters with *L.g. splendida* except in the number of supralabials. Only 4.4% of the specimens examined possess 8 supralabials. Allowing, however, for individual variation in this character, *L. catalinensis* Van Denburgh and Slevin is identical with and therefore should be considered a synonym of *L.g. splendida* (Baird and Girard).

L.g. splendida intergrades over a broad geographic area with *L.g. holbrooki* (Fig. 10). Specimens from the eastern portion of the range of *L.g. splendida* tend to have a pattern of irregular crossbands and a blotched venter (pattern 22, Fig. 31). Farther east, the pattern becomes intermediate as the scales between the dorsal bands develop spotting (pattern 21, Fig. 31) until the pattern becomes more like *L.g. holbrooki*. The influence of *L.g. splendida* on the *L.g. holbrooki* pattern 11 is apparent in the formation of dorsal bands (similar to pattern 13) which become more prominent in specimens from farther west (similar to patterns 14 and 15). Since specimens from this eastern part of the intergrade zone appear similar to *L.g. holbrooki* in pattern, populations in Kansas and Oklahoma have been identified as *L.g. holbrooki*. Webb (1970) stated that "characteristics applicable to *splendida* have been noted in some individuals of *holbrooki*. Five of 71 Oklahoma specimens have 23 scale rows

at midbody (*splendida*) but some *holbrooki* have 23 instead of 21 scale rows (Blanchard, 1921: 25, 34, 105)." He further stated that the two subspecies "may intergrade in southwestern Oklahoma." H.M. Smith (1956) stated that specimens of *L.g. holbrooki* from southwestern Kansas approach *L.g. splendida* in color pattern, but in other respects are typical of *L.g. holbrooki*. Nonetheless, neither author recognized an intergrade zone in their respective states.

Blanchard's (1921) statements that *L.g. holbrooki* sometimes has 23 dorsal scale rows were based on specimens from the intergrade zone described above. Specimens from this zone in Kansas, Oklahoma, and central Texas may have either 21 or 23 dorsal scale rows. In addition, the number of intergenials may be either 1 + 2 (59.4%) or 2 + 2 (35.5%). This is intermediate between *L.g. holbrooki* (83.1% have 1 + 2, only 6.6% with 2 + 2) and *L.g. splendida* (62.0% have 2 + 2, only 10.2% with 1 + 2). As would be expected in an intergrade zone, occasional specimens appear to have the pattern of either one form or the other. KU 16920 from 8 miles NE Clay Center, Clay County, Kansas, has pattern 23 (*L.g. splendida*), with the anterior part of the body intermediate between pattern 21 and 23 (influence from *L.g. holbrooki*). UMMZ 72357 from Osborne County, Kansas, has a pattern typical of *L.g. splendida* (pattern 23) except that the venter is blotched. This specimen also has only 21 dorsal scale

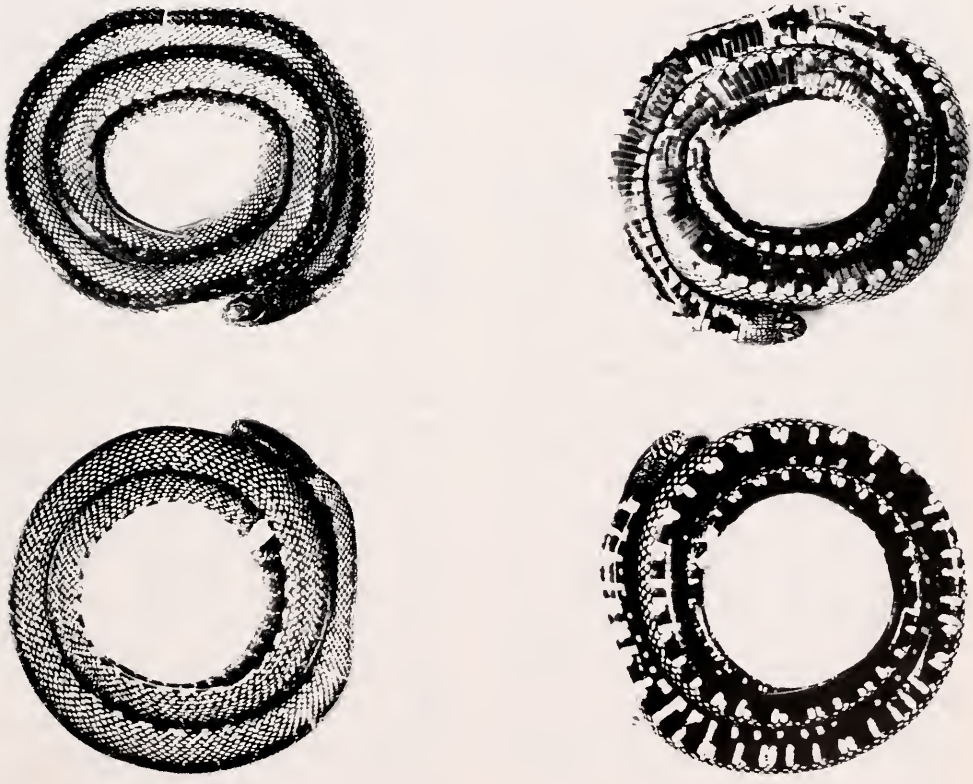


Figure 30. *Lampropeltis getulus splendida*. Top row dorsum and venter of CAS 50514, the holotype of *L. catalinensis*, from Santa Catalina Island, Gulf of California, Mexico; bottom row, dorsum and venter of LACM 3215 from 2 miles W Las Cruces, Dona Ana County, New Mexico.

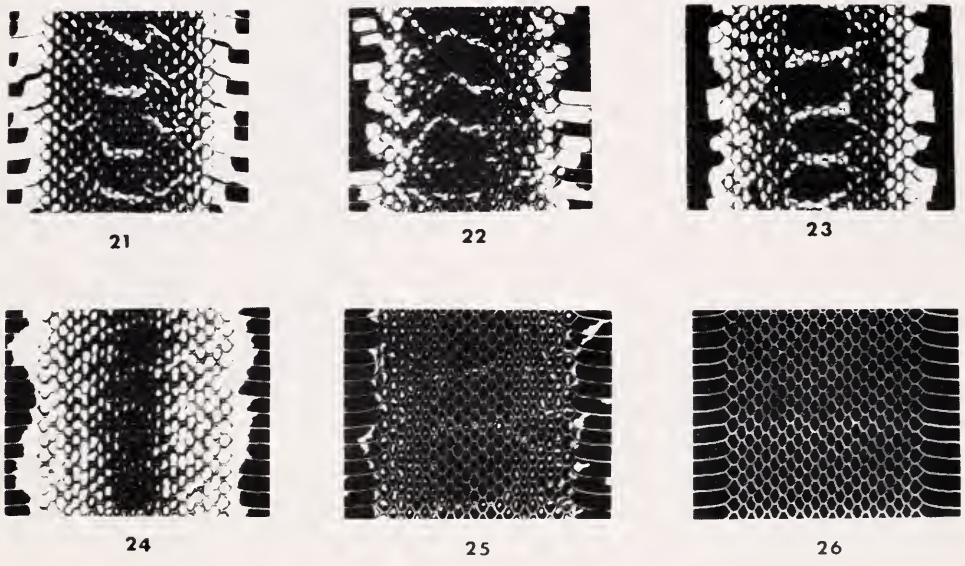


Figure 31. Basic pattern types of the western representatives of the *splendida* complex of *Lampropeltis getulus*. Pattern 21, intergrade between *L.g. splendida* and *L.g. holbrooki*; patterns 22 through 24, *L.g. splendida*; patterns 25 and 26, *L.g. nigritus*.

rows and 1 + 2 intergenials. This is also the case for UIMNH 18271 from 2 miles E Kearney County, Kansas. A specimen (UMMZ 126340), from 2.5 miles S Springer, Carter County, Oklahoma has a pattern intermediate between 21 and 23. One specimen (OSU R-161) from 4 miles N and 2 miles E Stillwater, Payne County, Oklahoma, is typical of *L.g. holbrooki* (pattern 11) but all other specimens from this area either show influence of *L.g. splendida* (pattern between 21 and 11), as, for example, OSU R-273 from Stillwater, Payne County, or show equal influence of both *L.g. splendida* and *L.g. holbrooki* (pattern 21, Fig. 31), as, for example, TNHC 4300 from Stillwater.

A specimen with data given as Bridges Pass, Wyoming (USNM 1715) is also considered an intergrade. It is a juvenile male with a pattern that appears to be intermediate between the juvenile patterns of *L.g. splendida* and *L.g. holbrooki*. The intergenials number 2 + 2. Since no additional specimens have been reported from this area or nearby, the locality data are questionable.

Lampropeltis getulus nigritus Zweifel and Norris

Lampropeltis getulus nigritus Zweifel and Norris, 1955: 238.
Lampropeltis getulus nigrita: Smith and Taylor, 1966: 23.

Holotype.—MVZ 50814 collected by Kenneth S. Norris and Richard G. Zweifel at 30.6 road miles south of Hermosillo, Sonora, Mexico.

Definition.—A subspecies of *L. getulus* characterized by a uniform black dorsum or a black ground color on which some dorsal scales and each lateral scale have a very small spot, 23 or 25 dorsal scale rows, anterior genials usually longer than posterior genials, 2 + 2 or 2 + 3 intergenials, a variable shaped loreal, and a moderately bilobed hemipenis.

Range.—Western Sonora and extreme northwestern Sinaloa, Mexico.

Description.—The following meristic and mensural data for this subspecies are based on a small sample of only 6 males and 7 females: ventrals 213 to 225 in males, 214 to 225 in females, subcaudals

52 to 56 in males, 47 to 51 in females; infralabials 9 (54.0%; or 10 (46.0%); loreal square (30.8%), slightly longer than high (30.8%), higher than long 23.0%), occasionally slightly higher than long (7.7%) or longer than high (7.7%); intergenials 2 + 2 (63.7%) or 2 + 3 (36.3%); anterior genials longer than posterior genials 42.8%), slightly longer (28.6%), or equal (28.6%); tail length 14.2% (14.1-14.4%) of total length in three males, 13.4% in one female; snout length 29.1% (28.4-29.9%) of head length in two males, 30.1% in one female.

The pattern is a reduced *L.g. splendida* pattern (pattern 25, Fig. 31), sometimes being so reduced that there is no visible pattern and the animal is uniformly black both dorsally and ventrally (pattern 26, Fig. 31). The anal plate, however, is always light colored.

Discussion.—Zweifel and Norris (1955) described *L.g. nigritus* as a subspecies which differs "from all other forms of *L. getulus* in its uniform dark brown or slaty black dorsal coloration without any trace of rings or stripes and in its high dorsal scale count." Of the 13 specimens of this subspecies examined, only two have the uniformly dark pattern 26 (Fig. 31). All others show the reduced *L.g. splendida* pattern 25 (Fig. 31). This condition is analagous to that found in *L.g. niger* with regard to the reduced *L.g. holbrooki* pattern. The high dorsal scale count reported by Zweifel and Norris (1955) resulted from their beginning their examination anterior to one head-length posterior to the head. Furthermore, occasional specimens of *L.g. splendida* also have 25 dorsal scale rows. The incidence of 25 scale rows, however, does appear to be greater in *L.g. nigritus*.

Hardy and McDiarmid (1969) reported two specimens from northern Sinaloa, Mexico, which they described as "similar to a specimen reported by Zweifel and Norris (1955: 239-40) as an intergrade between *L. getulus nigritus, L.g. splendida,* and *L.g. yumensis*." LACM 28715, one of the two specimens reported by Hardy and McDiarmid (1969) from 6 miles E Los Mochis, has a pattern only slightly bolder than pattern 25. Another specimen (LACM 52511), from 25.6 miles S Los Mochis, Sinaloa, is a large adult male (snout-vent length 1077 mm) with a typical *L.g. splendida* pattern 23. This suggests that *L.g. splendida* populations may occur south and east of this locality. Otherwise, the nearest locality for *L.g. splendida* is 6 miles E Santa Barbara in southern Chihauhua (AMNH 67731). The northern Sinaloa specimens probably represent intergrades between *L.g. splendida* and *L.g. nigritus*. All specimens north of Sinaloa to the northern third of Sonora are typical *L.g. nigritus*. Even juveniles such as USNM 148562 from 6 miles S Navajoa, Sonora, have the characteristic black pattern.

The northern one-third of Sonora and southeastern Arizona (Pima, Santa Cruz, Cochise, and southern Graham counties) is considered an intergrade zone in which specimens intermediate between *L.g. splendida* and *L.g. nigritus* are found (pattern types intermediate between 23 and 25). Within this area, specimens may have either a pattern typical of *L.g. splendida* (23) as UAZ 25127 from Cananea, Sonora, or *L.g. nigritus* (25) as AMNH 100628 from Fronteras, Sonora, or intermediate as EAL 141 from 4 miles N Nogales, Santa Cruz County, Arizona. Ecological preferences may allow the two subspecies to interdigitate in Sonora; *L.g. splendida* may occur along irrigation canals whereas *L.g. nigritus* may be confined to the desert.

Intergrades between *L.g. splendida* and *L.g. nigritus* have been found in scattered localities in southeastern Arizona as far north as Pima County (UAZ 22052 from Riletto Wash, Mt. Lemmon Road) and Cochise County (UAZ 25064 from 10 miles W Douglas). Influence of *L.g. nigritus* in Graham County has also been found and is discussed under the relationships of the *splendida* complex with the *californiae* complex.

The shape of the loreal scale cannot be used as a criterion for distinguishing either intergradation or relationships. Zweifel and Norris (1955) commented

that the shape of the loreal, being somewhat longer than high in the two specimens of *L.g. nigritus* examined, "suggests relationship to *yumensis*, while the ventral counts are suggestive of *splendida*." They added that "the presence of brown centers in dark brown lateral body scales is possibly indicative of a relationship to the speckled condition of *splendida*." The loreal shape is too variable to be a reliable character. In addition, 22% of the specimens of *L.g. splendida* examined have a loreal which is longer than high.

There are still too few specimens of *L.g. nigritus* available. None the less, unless additional collecting in southern Sonora reveals specimens with the *L.g. splendida* pattern, the differentiation of this population is sufficient to warrant its recognition as a valid subspecies of *L. getulus*.

The *californiae* Complex

Lampropeltis getulus californiae (Blainville)

Coluber californiae Blainville, 1835: 292.
Ophibolus boylii Baird and Girard, 1853: 82.
Coronella balteata Hallowell, 1853: 236.
Lampropeltis boylii conjuncta Cope, 1861: 301, 305.
Coronella pseudogetulus Jan, 1863: 238, 247.
Coronella getulus californica: Jan, 1865: Part 14, Pl. 5, Fig. 3.
Ophibolus getulus conjunctus: Cope, 1875: 37, 92.
Ophibolus getulus eiseni Yarrow, 1882: 439.
Lampropeltis nitida Van Denburgh, 1895: 143.
Lampropeltis boylei: Atsatt, 1913: 41.
Lampropeltis getulus yumensis Blanchard, 1919: 70.
Lampropeltis californiae nitida: Blanchard, 1920: 3.
Lampropeltis getulus conjuncta: Blanchard, 1920: 4.
Lampropeltis getulus californiae: Klauber, 1936: 18.

Holotype.—None designated. Type locality given as "California" restricted to the vicinity of Fresno by Schmidt (1953).

Definition.—A subspecies of *L. getulus* characterized by 21 to 44 light crossbands or a vertebral stripe on a ground color of chocolate brown to black, 23 or 25 dorsal scale rows, anterior genials usually longer than the posterior genials, 2 + 3 intergenials, a longer than high loreal, and a moderately bilobed hemipenis.

Range.—Southwestern Oregon southward to extreme southern Baja California, and eastward to southern Utah and the western half of Arizona.

Description.—Ventrals 213 to 250 in males, 213 to 255 in females; subcaudals 46 to 63 in males, 44 to 57 in females; infralabials 9 (66.8%) or 10 (30.8%), rarely 8 (1.2%) or 11 (3.1%); loreal usually longer than high (44.5%), slightly longer than high (15.5%), or square (33.1%), rarely higher than long (4.3%); intergenials usually 2 + 3 (55.0%), sometimes 2 + 2 (38.0%), rarely 2 (2.8%), 1 + 2 (1.8%), 2 + 4 (1.5%), 3 (0.5%), 3 + 4 (0.2%), or 1 + 3 (0.2%); anterior genials usually longer than posterior genials (52.3%), sometimes slightly longer (26.3%) or equal (21.2%), rarely less (0.2%); tail length 13.1% (11.4-15.1%) of total length in males, 12.2% (10.5-14.3%) in females; snout length 31.1% (27.9-33.7%) of head length in males, 30.7% (28.3-33.8%) in females.

The pattern is variable and consists of two types—longitudinal stripes or dorsal crossbands. Specimens with the striped pattern occur sympatrically with the banded pattern form.

In Oregon, California, Nevada, Utah, most of Arizona, and Baja California del Norte, specimens possess the banded pattern 27 (Fig. 33) in which the scales of the bands are entirely white or yellow (Fig. 32). In occasional specimens, the dorsal bands do not extend onto the venter but stop on the first scale row (pattern 28, Fig. 33) leaving the venter uniformly black. The bands may be connected along the first scale row to form lateral stripes. Specimens from southwestern Arizona, southern California, and Baja California (especially Baja California del Sur) usually have a pattern in which the scales of the dorsal bands are dark edged (pattern 29, Fig. 33). In southern Arizona, these bands may be narrow (pattern 30, Fig. 33).

The striped pattern 32 (Fig. 33) is found on specimens from southern

California and Baja California del Norte. The venter is usually light, but the dark edges of each ventral scute may extend farther toward the midline. Pattern 31 (Fig. 33) differs from the preceding primarily by the absence of lateral spotting (replaced by lateral stripes) and possession of a uniformly dark venter. Specimens with this pattern are found only in southern Baja California del Sur.

Discussion.—Although distinctive pattern types are found among populations of *L.g. californiae*, the division of these populations into subspecies cannot be justified. Pattern variation is either clinal or more than one type occurs within a single population.

Blanchard (1919) described *L.g. yumensis* as differing from the typical banded form (*L.g. boylii*) in that the scales of the bands "are shaded basally with brown, thus giving a spotted appearance to the light annuli," patterns 29 and 30 (Fig. 33). Klauber's (1936) concept of *L.g. yumensis* was somewhat more restrictive than Blanchard's (1919) description. Klauber characterized this subspecies, based primarily on specimens from the vicinity of Yuma, as having a pattern in which "the light rings are narrow and only the centers of the scales in these rings bear the light color." Specimens of this pattern (30) represent the greatest reduction of the basic banded pattern (27) and, especially in the vicinity of Yuma, may be the result of influence from *L.g. nigritus*, as is discussed under the relationship of the *californiae* complex to the *splendida* complex, below. Between Tucson and Yuma, many specimens possess a pattern of broader bands but with the same spotted appearance (pattern 29, Fig. 33). The distribution of these pattern types, of the continuous banded pattern (27), and of patterns intermediate between types 27 and 29, is shown in Fig. 34. It is obvious that the distributions of the two patterns broadly coincide, and that *L.g. yumensis* should not be recognized.

Figure 32. *Lampropeltis getulus californiae* from Cottonwood, Yavapai County, Arizona (specimen not available).

The population of banded kingsnakes in the Cape region of Baja California del Sur has been recognized as a distinct subspecies, *L.g. conjuncta* (Cope). The dorsal pattern is identical to that of *L.g. yumensis* (pattern 29), but the two forms were said to differ in that the "white bars on the prefrontal plates are oblong and occupy not more than one-half the area of these scutes" in *L.g. yumensis*, and "furthermore, in *L. getulus conjuncta* the infralabials are usually 10, and in *L. getulus yumensis* they are usually 9" (Blanchard, 1919). I have found that the width of the prefrontal bars decreases clinally from northwest to southeast. Even in central California, however, specimens with pattern 29 also have a more reduced prefrontal bar than specimens with pattern 27 from the same locality. This follows because the dorsal pattern reduction is due to increased melanin, and other pattern features, including the prefrontal bar, are likewise reduced. The banded populations in southern Baja California also have a reduced prefrontal bar (occupying 50 to 70% of the prefrontal scale compared with 80 to 95% in banded specimens with pattern 27), but the reduction is not so great as in southern Arizona. The latter may be the result of the influence of *L.g. nigritus*. The difference in the number of infralabials must be discounted. As was discussed above (variation in infralabials), all the populations in Baja California, including specimens with continuous bands in Baja California del Norte, have an unusually high incidence

of 10 infralabials (more than 50% of the specimens examined). Hence, the southern Baja California population does not differ significantly from populations in southern Arizona and California, and therefore should not be recognized as distinct.

Occasional specimens of *L.g. californiae* are found with pattern 28 (Fig. 34). Some specimens with this pattern type have the lateral edges of the bands expanded to form a pair of lateral stripes (*i.e.*, MVZ 64873 from 1 mile W Michigan Bar, Sacramento County, California) and were considered to belong to the striped species, *Lampropeltis californiae*, by Blanchard (1921) and Van Denburgh (1922). This pattern formed the basis of the description of *Ophibolus getulus eiseni* Yarrow, 1882. It is apparent that this form of striping is not homologous with the striping found in specimens in southern California (pattern 32), but rather is aberrant and derived from the typical banded pattern 27. Localities for specimens exhibiting this pattern are shown in Fig. 35.

The striped patterns 31 and 32 are found in southern Baja California and southern California, respectively (Fig. 35). Patterns intermediate between these patterns and the sympatric banded patterns are found in the same localities. Klauber (1936, 1939, 1944) provided considerable evidence that the striped form (*Lampropeltis californiae*) and the banded form (*Lampropeltis getulus boylii*) are pattern phases of a single subspecies, *L.g. californiae*. His conclusions were based primarily on a large series of broods from San Diego County, California, in which both pattern types appeared regardless of the pattern types of the mother. By analogy, Klauber (1936) suggested that *L. nitida* of southern Baja California was a pattern phase of *L.g. conjuncta*. However, since he also questioned the validity of *L.g. conjuncta*, he suggested "that all of these king snakes should be referred to as *L.g. californiae*." A specimen of *L. getulus* (LACM 21450) from Los Martiles, 5 miles S Buena Vista (Rancho), Baja California del Sur, Mexico, has a mixed pattern of

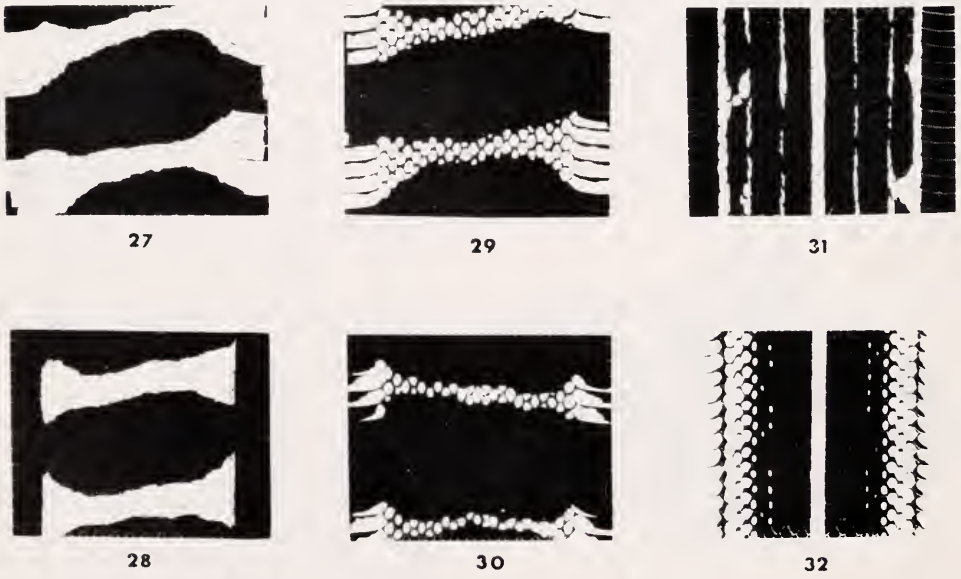


Figure 33. Basic pattern types of the *californiae* complex of *Lampropeltis getulus*. Striped and banded patterns of *L.g. californiae*.

crossbands and stripes, much like the mixed pattern found on some specimens in southern California, except that the venter is dark. Anteriorly, three bands (pattern 29) are complete; posteriorly, the dorsal stripe is broken in several places, but the pattern is essentially like pattern 31. The presence of this mixed pattern supports Klauber's contention that *L. nitida* is a pattern phase of the southern Baja California banded form. Thus, all of these populations are considered to be *L.g. californiae*.

Soule and Sloan (1966) reported *L.g. californiae* from several islands in the Gulf of California. Two specimens (SDSNH 44631 and 44632) from the northern end of Monserrate Island, Baja California del Sur, are typical of the southern Baja California population (pattern 29). The number of ventrals, however, is higher (223 on SDSNH 44631, a male, and 240 on SDSNH 44632, a female) and there are more dorsal bands (39 on each). In addition, shed skins were found on three islands in the northern Gulf of California: SDSNH 19989 from Isla Angel de la Guarda; SDSNH 45003 from Salsipuedes Island; SDSNH 45150 from Isla San Lorenzo Norte. SDSNH 19989 and 45003 clearly are *L.g. californiae* and pattern 29 can be detected in the shed skins. However, SDSNH 45150 does not have a distinctive pattern of crossbands. The skin appears to have come from a snake with a light venter (except for the lateral margins of the ventral scutes which are dark), light lateral scales, and a dark vertebral stripe. Other characteristics indicate that the skin came from a *Lampropeltis*, but its identification remains questionable.

Another kingsnake was reported from Cerralvo Island, east of La Paz, as *Lampropeltis getulus conjuncta* (Figg-Hoblyn and Banta, 1957). This specimen (not examined) appears to agree with the population on the adjacent mainland.

Klauber (1939) submitted the proposition that the populations of kingsnakes on southern California and northern Baja California which had the potential to "produce striped and aberrant pattern phases" might be recognized as a distinct

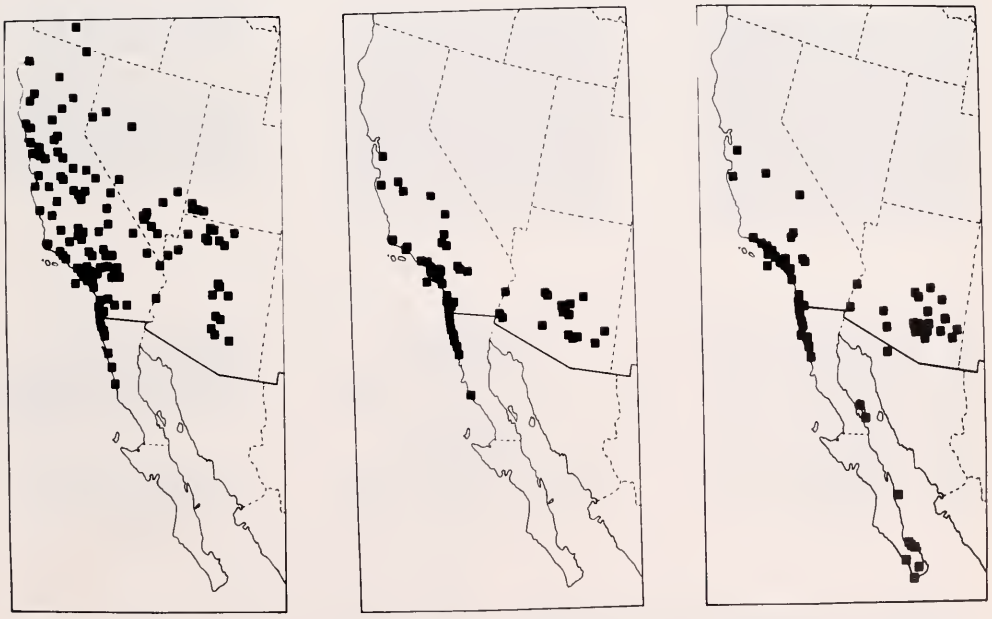


Figure 34. Distribution of the banded pattern types of *Lampropeltis getulus californiae* (left, pattern 27; right, pattern 29; middle, patterns intermediate between patterns 27 and 29).

subspecies. He presented one objection, however, with which I completely agree, that the classification of banded individuals would be based entirely on locality. Hence, I consider all of these populations to be *L.g. californiae*, a highly variable subspecies in which slight differentiation of the pattern has resulted in some recognizable populations. However, the degree of differentiation, relative to other subspecies within *L. getulus*, is at most at the level of the microgeographic race. The significance of the striped and banded pattern types is discussed in the conclusion section.

Relationships with the *splendida* Complex

Intergradation between *L.g. californiae* and members of the *splendida* complex occurs in southeastern Arizona and the southern Colorado River basin. Thirty-eight intergrades have been examined from this narrow zone.

L.g. californiae and *L.g. nigritus* intergrade along the Colorado River Valley and in southeastern Arizona. Such intergrades exhibit a darkened *L.g. californiae* pattern (pattern 33, Fig. 36) and have been found as far north as Parker, Yuma County, Arizona (ASU 4313). Three other specimens in the Colorado River Valley (UMMZ 69656 from the Gila Valley, near Yuma, Yuma County, Arizona; MVZ 32009 from the Laguna Dam, Potholes, Imperial County, California; and LACM 21449 from immediately west of the Río Colorado on Mexico Route 2, Baja California del Norte, Mexico) are unquestionably intergrades (pattern 33). However, eight additional specimens from the Colorado River Valley are typical *L.g. californiae* (pattern 29): KU 90837, UAZ 25084-25085, and MCZ 27107, all from Yuma, Yuma County, Arizona; UIMNH 38729 from 1.5 miles E Laguna, Yuma County, Arizona; MVZ 49932 from 7.3 miles SSW Imperial Dam, Imperial County, California; LACM 21437 from 5 miles S Alligator Slough (north of Blythe); and MVZ 5543 from 14 miles NE Blythe, Riverside County, California.

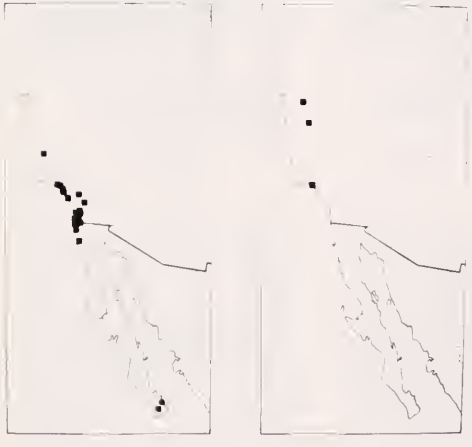


Figure 35. Distribution of the striped and black-bellied banded patterns of *Lampropeltis getulus californiae*. Left, the striped patterns 31 (circles) and 32 (squares); right, pattern 28.

The narrow bands (pattern 30) found on some specimens of *L.g. californiae* may reflect the influence of *L.g. nigritus* populations to the south. However, some specimens with the continuous banded pattern 27 also have narrow bands (*i.e.*, ASU 308 from Phoenix, Maricopa County, Arizona), and pattern 30 is also found as far north as Phoenix (*i.e.*, SM 1708).

Three specimens from Pima County, Arizona (ASDM 1919 from near Sasabee, UAZ 25075 from 0.6 miles W Robles P.O., and UAZ 28605 from Tucson) have a darkened *L.g. californiae* pattern typical of intergrades with *L.g. nigritus* (pattern 33).

Intergrades between *L.g. californiae* (pattern 29) and *L.g. splendida* (pattern 23) typically have broad dorsal crossbands which fork laterally, and spotting between the bands on the lateral scale rows (pattern 34, Fig. 36). Specimens with such a pattern have been examined from Pima, Cochise, and Graham counties, Arizona. Among 61 specimens examined from the vicinity of Tucson, Pima County, 41% have pattern 29, 36% have pattern 34 (intergrades), 6.5% have pattern 33 (intergrades), 11.5% have pattern 23 or a pattern intermediate between 23 and 25, and an additional 5% have a darkened pattern 34 (three way intergrades between *L.g. californiae*, *L.g.*

nigritus, and *L.g. splendida*: LACM 52518 from 2.5 miles S Sahuarita, UAZ 25641 and 28574 from Tucson).

In Cochise County, only 8 of the specimens are intergrades between *L.g. californiae* and *L.g. splendida*, whereas 70% are either *L.g. splendida* (10 specimens), *L.g. splendida* X *L.g. nigritus* (8 specimens), or *L.g. nigritus* (1 specimen). The following specimens from Cochise County are cited:

L.g. californiae X *L.g. splendida*—SE Willcox near the Chiricahua Mountains (LACM 58902); 11.5 miles SW Willcox (UAZ 25074); 4 miles NE Chiricahua (UMMZ 83967); 2.5 miles E Pearce (UMMZ 102435); 5 miles NNW Pearce (KU 68922); 4 miles SSE Cochise (AS 118); 4 miles SW Portal (UMMZ 83967); 24 miles E Dos Cabezas (LACM 20353).

L.g. splendida—1 mile S McNeal, Rt. 666 (ASDM 1256-1258); 2.5 miles S Rodeo (UAZ 31293); 15 miles S Rodeo (KU 6652); 1.6 miles W Pearce (UAZ 25057); Apache (UAZ 25051); Bisbee (UNM 12148); 16.6 miles N Douglas (LACM 34919); 10 miles SE Willcox (UMMZ 71343).

L.g. splendida X *L.g. nigritus*—Hereford (KU 48929); 15 miles S Rodeo (KU 6651); 8 miles SW, 9.7 miles SSE Willcox (LSUMZ 23271); 0.6 miles N Bernadino (LSUMZ 8928); 1 mile NW St. David (LSUMZ 9994); 10 miles W Douglas (UAZ 25064); 1.3 miles NE Chiricahua (UAZ uncatalogued); 3.5 miles W Rt. 666, S McNeal (ASDM 1596).

L.g. nigritus—Hereford (KU 48927).

From Graham County, one specimen of *L.g. californiae* (UAZ 25050 from 6 miles S Safford), one specimen of *L.g. splendida* (UAZ 25096 from 5 miles S Safford), one intergrade between *L.g. californiae* and *L.g. splendida* (UIMNH 24558 from 5 miles S Safford), and one intergrade between *L.g. californiae* and *L.g. nigritus* (AMNH 95953 from 5 miles N Solomon on the north bank of the Gila River) have been examined.

Thus, southeastern Arizona is an area of intergradation between *L.g. californiae*, *L.g. splendida*, and *L.g. nigritus*. The scattered records in a relatively narrow area, however, reflect the divergence of the two groups.

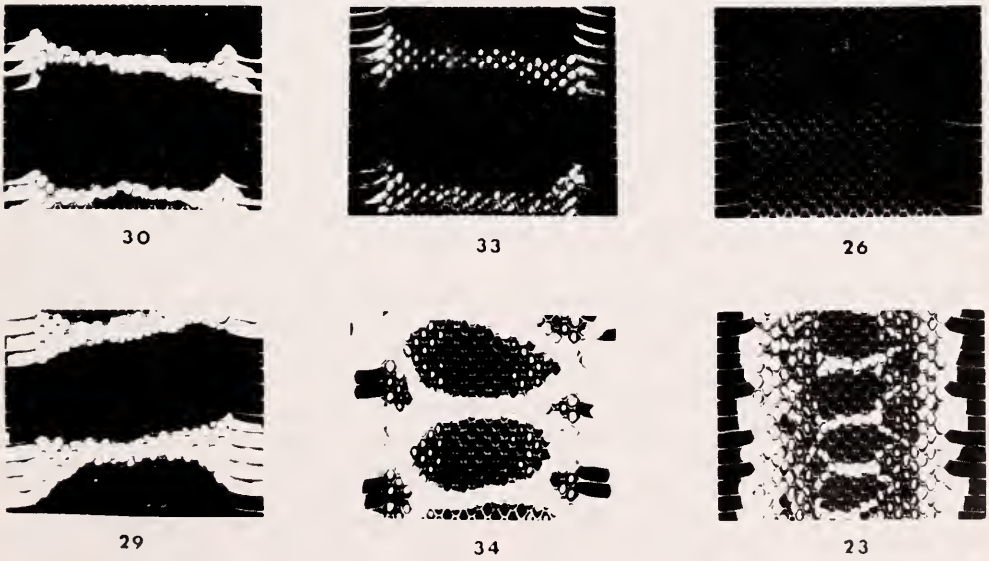


Figure 36. Pattern types of intergrades between *Lampropeltis getulus californiae* and members of the *splendida* complex. Pattern 29, *L.g. californiae*; pattern 33, intergrade between *L.g. californiae* and *L.g. nigritus*; pattern 34, intergrade between *L.g. californiae* and *L.g. splendida*; pattern 26, *L.g. nigritus*; pattern 23, *L.g. splendida*.

SUMMARY AND CONCLUSIONS

Color pattern is the primary feature on which I base my hypotheses about ancestral *Lampropeltis getulus* populations. Theoretically, the primitive pattern must be one from which all other patterns could have been derived. I suggest that pattern 24, as exhibited by *L.g. splendida* is closest to the ancestral type. In addition, I regard the high number of dorsal scale rows in *L.g. splendida* as a primitive character and its hemipenial structure as both primitive and generalized. Consequently, I consider *L.g. splendida* to be closest to the ancestral line. Moreover, the geographic position that *L.g. splendida* now occupies is one from which most other populations could have dispersed and differentiated.

A very early radiation of *L. getulus* produced three distinct phylogenetic lines, the *getulus* complex in the east, the *californiae* complex in the west, and the centrally located *splendida* complex. A proposed phylogeny for *Lampropeltis getulus* is illustrated in Fig. 37.

The primitive pattern (24) of *L.g. splendida* has been modified slightly by the reduction of spotting between the dorsal bands to produce pattern 23. At the present time, only occasional specimens exhibit pattern 24. The differentiation of the other subspecies in the *splendida* complex has followed obvious lines. The evolution of *L.g. nigritus* in the Sonora Desert reflects a darkening of the *L.g. splendida* pattern but with no change in scutellation. The differentiation of *L.g. holbrooki* has involved slight modification of the primitive pattern, and a reduction in the number of dorsal scale rows and intergenials. The evolutionary processes of pattern neoteny and melanization produced *L.g. niger*.

The wide zone of intergradation between *L.g. holbrooki* and *L.g. splendida* in Oklahoma and Kansas may be the result of population displacement during the Late Wisconsin glaciation and the subsequent repopulation of an area of interdigitated deciduous forest and grassland habitats (Küchler, 1964). During the retreat of the glaciers, populations of both subspecies may have moved into this region. The result is a heterogenous series of populations with widespread intergradation.

The greatest distributional anomaly in the *splendida* complex is the presence of *L.g. splendida* on Santa Catalina Island in the Gulf of California, Mexico. Whether this record represents a relict population or a rafted or released individual remains to be proved. The possibility of there being a relict population on Santa Catalina Island seems remote since *L.g. californiae* occurs on Monserrate Island, just 15 miles west of Santa Catalina Island. This record must remain questionable until additional specimens become available.

Blanchard (1921) postulated that *L.g. getulus* was derived from *L.g. niger* by expansion of the light dorsal bands and that *L.g. floridana* evolved from *L.g. getulus* by "a basal lightening of each dark scale." His evidence for such a phylogeny, however, was based primarily on the geographic position of these forms. First, he considered that *L.g. getulus* was derived from *L.g. niger* because of similarity of pattern and because the two populations are adjacent. I have shown that his interpretation of pattern similarity is unwarranted; the reduced number of dorsal bands in *L.g. niger* is not an approach to the condition in *L.g. getulus*. Furthermore, the great difference in hemipenial structure between *L.g. getulus* and *L.g. niger* also eliminates *L.g. niger* as a probable ancestor. In addition, the lack of a wide zone of intergradation between the two forms indicates that *L.g. getulus* and *L.g. niger* are not closely related.

Within the *getulus* complex, I consider *L.g. floridana* to be closest to the ancestral stock, a direct derivative of the primitive *L.g. splendida* populations in Texas. I base this hypothesis on both populations having a maximum of 23 dorsal scale rows, and similarities in dorsal pattern. The *L.g. floridana* pattern is interpreted as being the result of an ontogenetic increase in scale spotting on

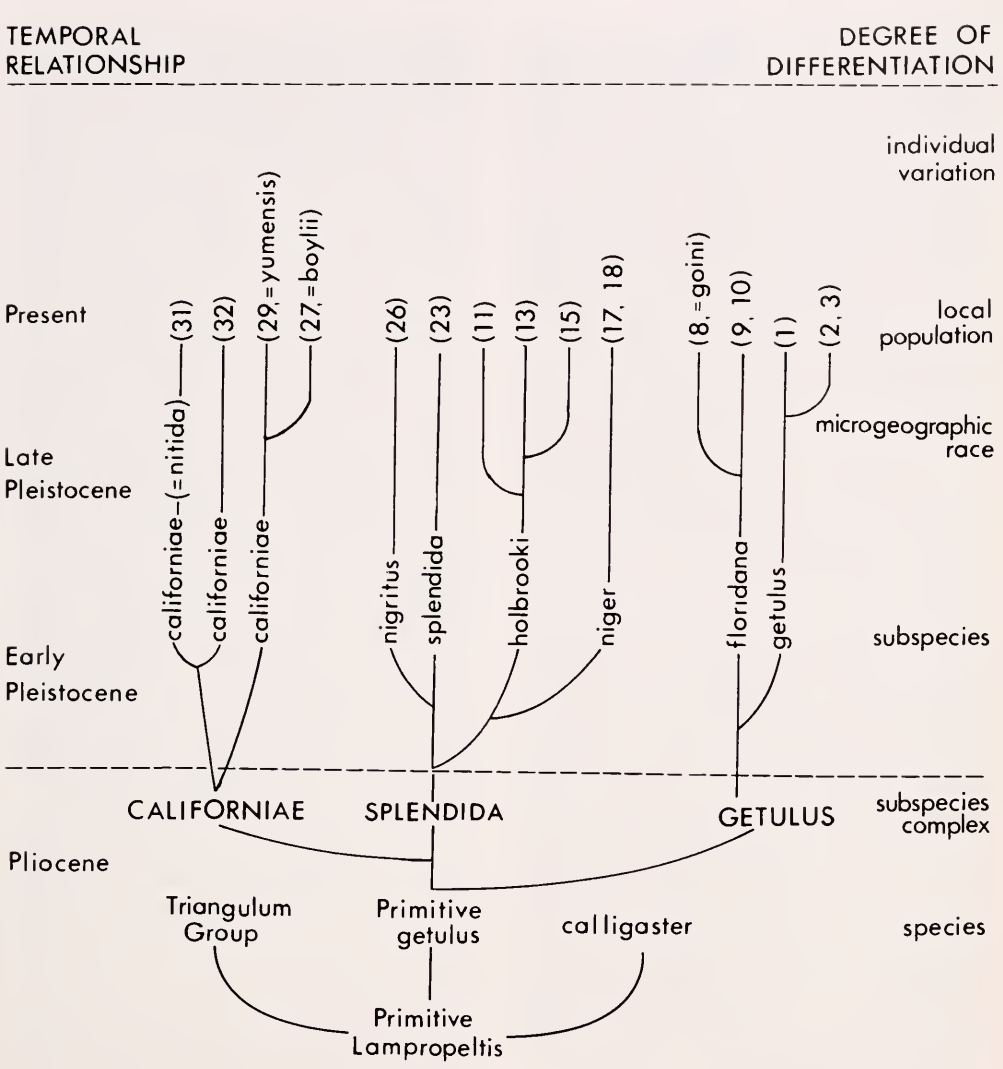


Figure 37. A proposed phylogeny for the subspecies and microgeographic races of *Lampropeltis getulus*. Numbers in parentheses at top refer to pattern types.

the basic primitive pattern. The pattern of *L.g. getulus* is the result of retention of the juvenile pattern of *L.g. floridana*. Additionally, *L.g. getulus* has fewer dorsal scale rows (21 compared with 23).

The geographic separation between *L.g. floridana* and *L.g. splendida* does not exclude the possibility of the proposed phylogenetic relationship. I suggest that the population ancestral to *L.g. floridana* (similar in pattern to *L.g. splendida*) expanded its range from the west into the land newly exposed by a reduction of Pleistocene sea level (Russell, 1964). Such a migration probably occurred during a glacial stage prior to the Wisconsin glaciation. It has been suggested that *Terrapene carolina* (Auffenberg, 1958; Blaney, 1971), *Coluber constrictor*, and *Masticophis flagellum* (Blaney, 1971) have also utilized such a Pleistocene migration route. The pres-

ence of disjunct populations of *L.g. floridana* in northeastern Florida and in the Apalachicola region suggest that *L.g. floridana* was once widespread throughout the peninsula. Rising seas of an interglacial stage then isolated the eastern (*L.g. floridana*) and western (*L.g. splendida*) groups by inundation of the continental shelf. Perhaps at the same time, spatial separation of the northern and southern extremes of the eastern group resulted in differentiation into the two subspecies now recognized (*L.g. getulus* and *L.g. floridana*). Partial inundation of the Okeefenokee region may have resulted in at least some degree of isolation of the two populations. During the successive glacial stage, the *L.g. floridana* population in the northern Florida peninsula moved south following suitable habitat. At the same time, the newly differentiated *L.g. getulus* moved into the northern part of the peninsula, intergrading with and replacing *L.g. floridana*, thus producing the wide zone of intergradation now observed. The *L.g. getulus* stock probably moved along the central highland region of Florida thus separating the northern populations of *L.g. floridana*—the Apalachicola population and the northeastern Florida population. The disjunct *L.g. floridana* population in the Apalachicola region has undergone some differentiation which is reflected in the wide dorsal bands, but, as discussed above, the population consists of intergrades and should not be given taxonomic recognition.

Additional evidence that it was *L.g. getulus* which differentiated from *L.g. floridana* is provided in the occasional individuals and populations (*i.e.*, the Outer Banks of North Carolina) which show characteristics of *L.g. floridana*. The populations of *L.g. getulus* have undergone a further differentiation into two microgeographic races, a piedmont and a coastal form. The populations in Maryland and Delaware are derived from the piedmont form. The New Jersey populations, on the other hand, are coastal plain derivatives.

The reduced amount of intergradation occurring between *L.g. getulus* and members of the *splendida* complex may be the result of the population displacements discussed above. *L.g. getulus, L.g. holbrooki*, and *L.g. niger* probably have expanded their ranges since the last glaciation. The populations of *L.g. holbrooki* and *L.g. niger* may be only now making contact with *L.g. getulus*.

The evolution of *L.g. californiae* has involved various modifications of the primitive *L.g. splendida* pattern. Blanchard (1921) used characteristics of intergradation as evidence for the evolution of *L.g. yumensis* (=*L.g. californiae*) from *L.g. splendida*. The banded pattern of *L.g. californiae* probably was derived in a fashion very similar to that which he described. The dorsal bands of *L.g. splendida* increased in length as the lateral spotting between the bands decreased, until the dorsal bands extended onto the ventral scutes. Within the *californiae* complex, therefore, I consider pattern 29 to be closest to the primitive banded pattern. The continuous banded pattern 27 is a further specialization of this basic pattern.

Concerning the striped pattern exhibited by *L.g. californiae*, Blanchard (1921) stated that this form (which he considered as a species) was derived from animals with the continuous banded pattern. He based this contention on the aberrant striped individuals that approach the continuous banded pattern. Blanchard presented the hypothesis that the striped pattern types resulted from a mutation of the continuous banded form, because the striped pattern apparently became differentiated within the range of its parent. Thus he said that the striped form originated "somewhere in the Great Valley of California. It spread southward west of the Sierra Nevada Mountains and the deserts of southwestern California, becoming more different from *boylii* toward southwestern California. From here it extended its range into Lower California to Cape San Lucas. At some point in this peninsula, probably pretty well south, it became modified into the color variety *nitida*." If one accepts the

well documented idea that the striped and banded patterns occur in a single species (Klauber, 1936, 1939, 1944), the above concept does not explain the fact that in San Diego County 90% of the kingsnakes exhibit either the banded or the striped pattern and only 10% have a mixed pattern, whereas populations to the north in Orange, Riverside, and Los Angeles counties are different in the relative abundance of these patterns. In the San Diego area, the striped pattern comprises about one third of the population, and the striped pattern outnumbers the mixed pattern by 3 or 4 to 1 (Klauber, 1936). In Orange, Riverside and Los Angeles counties, however, only 6% of the population show any tendency toward striping and the mixed pattern is five times more abundant than the striped pattern. The evolution of these striped populations that are sympatric with banded populations has also not been adequately explained.

Dunn (in Mayr, 1944) attempted to prove that the segregation of striped and banded pattern types indicated a simple Mendelian relationship involving a single pair of genes. The ratios within broods of banded mothers indicated that the banded pattern is dominant, but the progeny of striped mothers did not approach expected frequencies. Klauber (1936) showed that the young from banded mothers were mostly banded, whereas the young of a striped mother are mostly striped. Dunn (*loc. cit.*) included the aberrant patterns among the striped "because of the resemblance of the aberrant to the general features of the striped form" and stated that there was "no indication that the aberrants are hybrids." He neglected to note the fact that in populations immediately north of San Diego, the aberrant patterns are far more abundant. In these areas and in San Diego County, the so-called aberrant patterns range from banded with occasional bands broken (some of which may be oriented longitudinally) to essentially striped with the vertebral stripe broken (some of the smaller sections of the stripes may be oriented laterally). I do not recognize these patterns as aberrant, but rather as intermediate between the striped and banded patterns. The range of variation among specimens exhibiting the intermediate pattern indicates that more than a single pair of genes is responsible for the two pattern types, and therefore this phenomenon is not a simple pattern dimorphism. The full range of intermediate patterns between the two extremes indicates that there are at least two, and probably more, alleles responsible for pattern. Pattern modifying genes may cause varying degrees of expression of other genes. It appears, then, that there is no simple Mendelian relationship between the two pattern types.

The fact that few intermediates exist in San Diego County perhaps can be attributed to environmental factors that prevent the action of some pattern modifying genes. Thus, the pattern expression is an either-or situation with only occasional action of modifying genes resulting in only 10% of the population being intermediate. The populations in San Diego County therefore approach true pattern dimorphism. Elsewhere, because of the high incidence of intermediates, the situation is certainly not a simple dimorphism, nor can it be called polymorphism because the additional patterns are not something new, but rather something intermediate. Such a range of variation in pattern might be expected in a zone of intergradation between two subspecies.

I suggest, therefore, that the existence of these two very different pattern types may be the result of two different phylogenetic lines, and the intermediate specimens are actually the result of intergradation. Population movements and displacement may have resulted in these two lines competing for and occupying the same geographic area. Thus we may actually be observing what were once two subspecies occurring sympatrically at the present stage in their evolution.

Two lines may have diverged from the primitive *L.g. splendida* stock, the banded pattern type in the manner previously described and the striped

pattern by a rather simple modification of the *L.g. splendida* pattern. The dorsal bands of *L.g. splendida* need only to have become oriented longitudinally and the lateral spotting reduced slightly. The ventral coloration probably was dark primitively (retained in the populations in southern Baja California and occasional specimens in southern California), but became light as the pattern became more specialized. The striped populations probably became established in southern California and extended into Baja California. This striped population then became separated into southern California and southern Baja California populations, each of which differentiated, thus producing the two distinctive striped populations. Meanwhile, the banded populations differentiated farther east and north. Fluctuations in climate and sea level during the Pleistocene may have caused displacement of the banded populations.

The banded populations in southeastern California and southwestern Arizona may have expanded southward along the eastern coastal shelf (exposed during a glacial period in the Late Pleistocene) of the Baja California peninsula thus invading the southern part of the peninsula which was already occupied by a striped population. Evidence for such a hypothesis is the occurrence of *L.g. californiae* with pattern 29 on the islands in the Gulf of California. Perhaps at the same time, the central California banded populations expanded their range southward and invaded the territory already occupied by striped populations in southern California. In each case, the result is intergradation not at the periphery of the range of these forms, but within the range of the striped form. At present, then, we may be looking at the replacement of a striped population by a banded population.

Nomenclatural recognition of such a situation is impossible. Although it is possible to distinguish two populations of striped kingsnakes, both are found sympatrically with banded forms. In southern Baja California, the striped form (*L.g. nitida—L.g. californiae*) is found within the banded population (*L.g. conjuncta* = *L.g. yumensis* = *L.g. boylii* = *L.g. californiae*) similar to the population in southwestern Arizona. The southern California striped populations (*L.g. californiae*) are sympatric with banded forms having pattern types 27 and 29 (*L.g. boylii* and *L.g. yumensis* = *L.g. californiae*). Thus, to avoid recognition of sympatric subspecies, all populations must be regarded as part of a diphyletic subspecies, *L.g. californiae*.

Neill (1963) provided a substantial amount of information on the occurrence of striped patterns in the eastern subspecies of *L. getulus*, stating that the "lineate, '*californiae*' pattern is often suggested, and sometimes duplicated." Thus Neill (1963) postulated "that a single widespread species, *L. getulus*, has the genetic potentiality of producing a lineate pattern along with the more common ringed one." Many individuals of *L.g. getulus* have incomplete dorsal bands, perhaps half a band reaching only the middorsal scale row. The bands of others may be broken and longitudinally expanded. The lateral forking of the dorsal bands may be so prominent so as to form a continuous lateral line. The specimen illustrated by Neill (1963: 198 A) has an almost continuous vertebral stripe, but it is not identical to the vertebral stripe exhibited by *L.g. californiae*. A specimen from near Engelhard, Hyde County, North Carolina (NCSM 2019), also has an aberrant striped pattern. This specimen has no light dorsal bands, but rather has paired lateral blotches that are connected along the fourth scale rows on each side by a continuous light stripe. Thus, this specimen has a pair of dorsolateral stripes. It would appear, then, that the pattern of dorsal bands lends itself to aberrations that may take the form of longitudinal stripes.

Analysis of distribution.—The overall range of *L. getulus* may be limited by two factors: 1) competition with similar species; and 2) a reflection or Pleistocene displacement southward. The northern

extremes of the range may be the result of the displacement of the species southward during the Late Wisconsin glaciation in conjunction with thermal factors. *L.g. californiae* is not common in northern California and Oregon. The northern limits of *L.g. holbrooki* and *L.g. niger* may reflect glacial displacement followed by a slow recovery of territory. The distribution of *L.g. getulus* along the Atlantic coast may reflect the same phenomenon. There are records of *L.g. getulus* from Long Island (DeKay, 1842) and New England (Babcock, 1920). Babcock (1920) said, however, that the occurrence of *L.g. getulus* in Connecticut, based on a sight record, is doubtful. Nonetheless, it is possible that the range of *L.g. getulus* did extend this far north at one time, but that such populations are now extinct.

I suggest that the northern limits of *L.g. getulus, L.g. niger,* and *L.g. holbrooki*, and the southern limit of *L.g. splendida* in Mexico, may be affected by competition with populations of large-sized *Lampropeltis triangulum*. The large *L.t. triangulum* replaces *L. getulus* in the northeastern United States and *L.t. polyzona, L.t. arcifera, L.t. nelsoni,* and *L.t. sinaloae* replace *L.g. splendida* in Mexico (distribution based on Williams, 1970).

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March 25, 1977

ETHEOSTOMA ETNIERI, A NEW PERCID FISH FROM THE CANEY FORK (CUMBERLAND) RIVER SYSTEM, TENNESSEE, WITH A REDESCRIPTION OF THE SUBGENUS *ULOCENTRA*

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ABSTRACT

The subgenus *Ulocentra* is diagnosed and redescribed. *Etheostoma etnieri*, a new darter of the subgenus *Ulocentra* (Percidae, Etheostomatini), is described from the Caney Fork (Cumberland) River system in Tennessee and is compared with the nominal *E. atripinne*, *E. duryi* and *E. simoterum*. This brightly colored, sexually dichromatic darter is more closely allied to *E. duryi* than any other nominal *Ulocentra*. *Etheostoma etnieri* differs from *E. duryi* mainly in modal number of caudal peduncle scales and pigmentation of the body and fins and from Cumberland River basin *E. atripinne* in having fewer dorsal saddles, usually a poorly developed premaxillary frenum and in pigmentation of the body and fins. *Etheostoma etnieri* also has fewer lateral-line scales compared to *E. atripinne* from the Caney Fork River system. Range, relationship, size, fish associates and ecological data are presented.

Etheostoma etnieri represents one of three previously undescribed darters endemic to the Caney Fork River system of the Cumberland River basin (Bouchard 1973) and is one of seven presently recognized undescribed forms of snubnose darters within the state of Tennessee. In addition to *E. etnieri*, the Caney Fork River fauna includes a second member of the subgenus *Ulocentra* presently referable to *E. atripinne*. The subgenus is unique among darters, containing more undescribed than nominal species. The extreme morphological and meristic similarity between members of the subgenus has contributed to much of this taxonomic uncertainty. All four nominal species of *Ulocentra* occur within Tennessee waters.

Subgenus *Ulocentra* Jordan 1878:223
Snubnose Darters

Diagnosis—Group of closely related, medium sized, sexually dichromatic darters closely allied to subgenus *Etheostoma*, sharing with that group complete lateral-line and cephalic canal system, broadly connected gill membranes, expansive pectoral fins, declivous snout, distinct dorsal blotches or saddles, breeding males brightly colored, often with reds and usually greens. Phylogenetically more advanced subgenus *Ulocentra* generally differing from members of *Etheostoma* (*sensu stricto*) in following ways: breeding males lacking nuptial tubercles; branchiostegal rays 5 (6 in *E. coosae*); lateral line usually slightly arched anteriad; snout steeply declivous (slightly produced in *E. coosae* and *E. duryi*: see Figs. 5c,f); dorsal blotches or saddles typically 8 or 9 (rarely 7, 10 or 11); palatine teeth always absent; pelvic and anal fins melanistic in breeding males; spinous portion of dorsal fin often with red ocellus in first interradial membrane.

Description—Body slightly compressed; snout steeply declivous, less so in *E. coosae* and *E. duryi* (Figs. 5c,f); mouth subterminal, horizontal; frenum variable,

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absent to well developed. Eye breaking dorsal contour of head in lateral view; nape distinctly humped, often decurving sharply to occiput. Caudal fin slightly emarginate; branchiostegal membranes broadly connected, rays 5-5, in *E. coosae* 6-6; pectoral fin typically longer than head; eye length greater than snout. Lateral line complete, slightly arched anteriad; scales moderate in size (37-62 in lateral line); vertebrae 37-40. Dorsal fin spines IX-XIII; dorsal fin soft rays 10-13; anal fin spines II, first largest; anal fin soft rays 6-9; branched caudal fin rays 13-17; pectoral fin rays 12-15. Supratemporal canal complete with 3 pores; lateral canal complete with 5 pores; single coronal pore; postorbital, interorbital, posterior nasal and anterior nasal pores present; preoperculomandibular canal complete with 7-9 pores; infraorbital canal with 7-10. Nape, temporal areas, opercles, prepectoral region and belly covered with exposed scales. Breast naked or covered with exposed or embedded scales on posterior half (scales may extend from prepectoral regions along caudal margin of branchiostegal membranes mesiad, but not forming complete line of scales). Cheeks covered with embedded and/or exposed scales. Nuptial tubercles absent. Genital papilla sexually dimorphic, long subcylindrical tube in breeding females; much shorter and narrower, subconical to subcylindrical structure in breeding males. Dark subocular and preorbital bars, latter passing beneath anterior naris and may reach upper lip. Three or four small caudal spots, ventral member may be lacking, middle one(s) may be coalesced with lateral blotch. Lateral blotches 7-11, rounded or vertically elongate, may be discontiguous or fused into irregular lateral band. Dorsal blotches or saddles usually 8 or 9 (range 7-11 due to irregularities in distribution of dorsal pigments).

These medium sized darters inhabit riffles and runs of low to moderate turbulence. Preferring small to medium sized streams, their habitats range from springs to large rivers where they are less common and usually found near the margins. In areas draining well indurated rocks of Mesozoic or Paleozoic age, they are most often collected over gravel riffles with or without scattered rocks; runs may be gravel and/or sandy. Coastal Plain species predominantly occur over gravel and/or sandy riffles and runs. The subgenus is widely distributed over the southeastern United States in the Mississippi, Mobile Bay and some Gulf Coastal drainages. In the Mississippi drainage, members of the subgenus are known from the Kentucky River system downstream to the Yazoo River system. They are notably absent from the Mississippi Alluvial Plain and west of the Mississippi River. They occur in all major tributaries of the Mobile Bay drainage (*i.e.* Coosa, Tallapoosa, Black Warrior and Tombigbee River systems) and Gulf Coastal drainages east of Mobile Bay to the Choctawhatchee River system.

Etymology—oulos (Gr. = complete) in combination with *kentron* (Gr. = spine) in reference to the two well developed anal fin spines "the chief character separating the genus from *Boleosoma*" (Jordan and Evermann 1896:1047).

Type-species—Etheostoma atripinne [as *Ulocentra atripinnis* (Jordan 1878: 223)]. Type-species, by monotypy (see Jordan 1919:395).

List of species—Etheostoma atripinne (as *Arlina atripinnis* Jordan 1877:10). Etymology: *ater* (L. = black) in combination with *pinna* (L. = fin) in reference to the black pelvic and anal fins of breeding males, common in the subgenus.

Etheostoma coosae (as *Poecilichthys coosae* Fowler 1945:356). Etymology: "Named for the Coosa River" (Fowler 1945:358), from which basin the types were collected in Cherokee County, Alabama.

Etheostoma duryi Henshall 1889:32. Etymology: patronym in honor of its collector, Mr. Charles Dury.

Etheostoma etnieri new species, described herein.

Etheostoma simoterum (as *Hyostoma simoterum* Cope 1868:215). Etymology: *simos* (Gr. = snub-nose) and *ter* (Gr. =

suffix, signifying agent) in reference to the contour of the snout, common in the subgenus.

KEY TO SPECIES

1a Premaxillary frenum moderately to well developed, anterior margin of snout bound to upper lip by mesial fleshy bridge.....2

1b Premaxillary frenum poorly developed or lacking, anterior margin of snout free and often partially overhanging upper lip.....4

2a (1a) First two dorsal saddles anterior to spinous portion of dorsal fin (Fig. 2c).....*atripinne** Tennessee River system in Tennessee and Alabama upstream to Cumberland Plateau.

2b Only one dorsal saddle anterior to spinous portion of dorsal fin (Fig. 1c).....3

3a (2b) Breast usually with scales on posterior half; alternating broken pale and solid dark lines above lateral line.....*etnieri* That portion of Eastern Highland Rim drained by Caney Fork (Cumberland) River system.

3b Breast usually without scales on posterior half, lacking alternating broken pale and solid dark lines above lateral line.....*simoterum** Tennessee River system in Virginia, Tennessee and Alabama downstream to Sequatchie Valley.

4a (1b) Branchiostegal rays 6; spinous portion of dorsal fin with complete, bright red band in breeding males.....*coosae* Coosa River system in Tennessee, Georgia and Alabama above the Fall Line.

4b Branchiostegal rays 5; spinous portion of dorsal fin with bright red limited to ocellus in first interradial membrane.....5

5a (4b) Breast usually with scales on posterior half; alternating broken pale and solid dark lines above lateral line; caudal peduncle scales usually 18 or 19.....*etnieri* That portion of Eastern Highland Rim drained by Caney Fork (Cumberland) River system.

5b Breast usually without scales on posterior half; lacking alternating broken pale and solid dark lines above lateral line; caudal peduncle scales usually 17 or fewer.....*duryi* Tennessee River system in Tennessee and Alabama.

*See *RELATIONSHIPS* for discussion of *E. atripinne* and *E. simoterum*.

Etheostoma etnieri, new species
Cherry Darter

The description is based on 362 specimens collected from the Caney Fork (Cumberland) River system, Tennessee. Counts and measurements are those outlined in Hubbs and Lagler (1958) except for diagonal scale counts (Raney and Suttkus 1964). Head length was measured from the tip of the snout to the end of the opercular spine. A vernier caliper was used in making measurements to the nearest 0.1 mm. Measurements are expressed in thousandths of standard length unless otherwise indicated. The description of cephalic canals follows Hubbs and Cannon (1935) except the term preoperculomandibular has replaced operculomandibular. Vertebral counts were made from radiographs of 30 specimens following Bailey and Gosline (1955). Means for meristic and morphometric data are indicated in parenthesis. Most of the locality data in the *Material* section were derived from Tennessee General Highway County Maps, 1967 editions, for the following counties: Putnam, Van Buren, Warren and White. Specimen references as follows: AU-Auburn University, CU-Cornell University, TU-Tulane University, USNM-National Museum of Natural History, UT-University of Tennessee Ichthyology Collection. Parenthetic enclosures indicate the number of specimens in the numbered lot.

Material.—Holotype.--TU 83147, an adult male, 60.4 mm in standard length, collected 18 March 1972 at Cherry Creek, tributary to Calfkiller River [Caney Fork (Cumberland) River

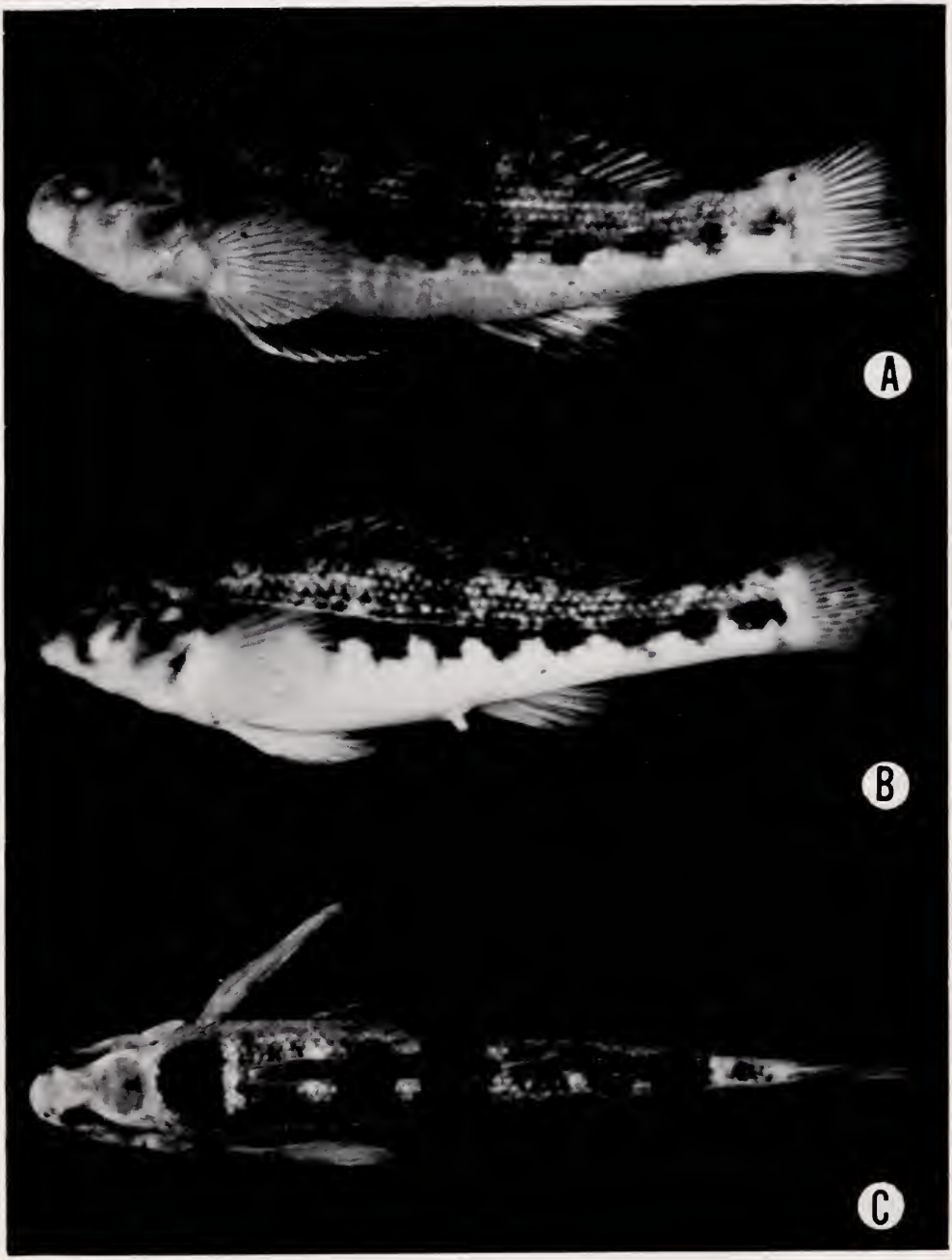

Figure 1. *Etheostoma* (*Ulocentra*) *etnieri*, sp. nov. a (top) Lateral view of holotype, adult male, S.L. 60.4 mm (TU 83147). b (middle) Lateral view of allotype, adult female, S.L. 47.8 mm (TU 83148). c (bottom) Dorsal view of a paratype, adult male, S.L. 55.8 mm (TU 83149).

Figure 2. *Etheostoma* (*Ulocentra*) *atripinne* from the Caney Fork River system, Tennessee (RWB 9-2469-3). a (top) Lateral view of adult male, S.L. 57.3 mm. b (middle) Lateral view of adult female, S.L. 50.2 mm. c (bottom) Dorsal view of adult male S.L. 57.3 mm.

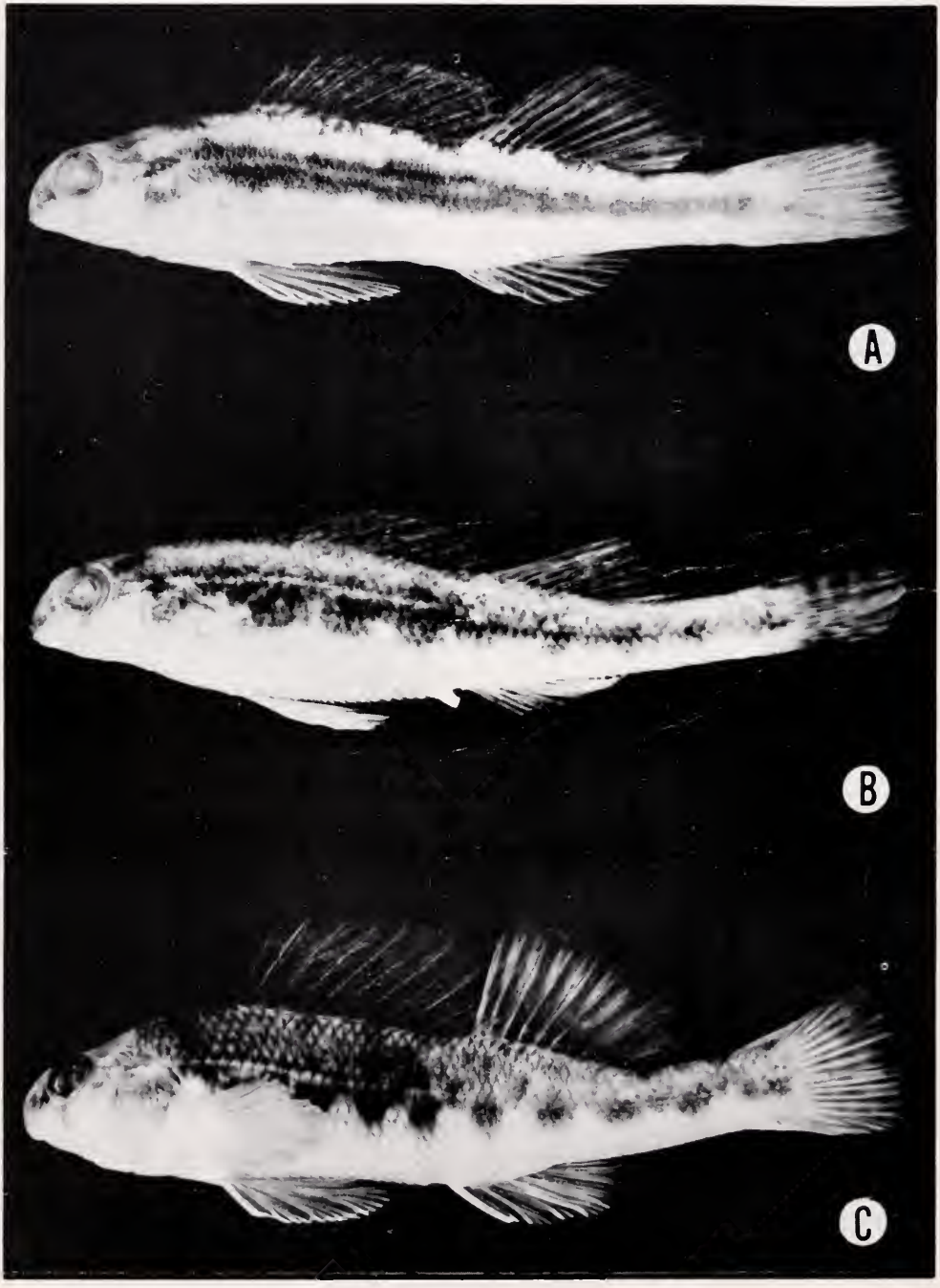

Figure 3. *Etheostoma* (*Ulocentra*) *duryi* from the Tennessee River system, Tennessee. a (top) Lateral view of adult male, S.L. 47.0 mm (UT 91.581). b (middle) Lateral view of adult female, S.L. 41.1 mm (UT 91.581). c (bottom) Lateral view of adult male, S.L. 50.8 mm (UT 91.628).

system], at Tennessee State Highway 84 (near Yankeetown Community), 5.3 miles northeast of intersection of U.S. Highway 70 and Tennessee State Highway 84 in Sparta, White County, Tennessee, by R.W. Bouchard, J.D. Way, F.L. Oakberg and B.E. Oakberg.

Allotype.--TU 83148, an adult female 47.8 mm SL, taken with the holotype.

Paratopotypes.--UT 91.211 (14), 5 October 1968; (22), 8 July 1969; USNM 214172 (56), 9 October 1971; TU 83149 (11), 18 March 1972; UT 91.677 (14), 6 June 1972.

Paratypes.--PUTNAM COUNTY, Calfkiller River along Tenn. St. Hwy. 84, SW of Monterey, lat. 35° 18-20' N, long. 85° 01-07' W, 6 June 1972, UT 91.672 (9). VAN BUREN COUNTY, Cane Creek, 5.4 mi. E Spencer at Tenn. St. Hwy. 30, lat. 35° 44-45' N, long. 85° 23-24' W, 16 July 1964, (1), TU 33451; Cane Creek at County Road 4251, lat. 35° 48-49' N, long. 85° 25-26' W, 8 July 1969, (3), Cane Creek at County Road 4251, 6 June 1972, (9), UT 91.676. WARREN COUNTY, Barren Fork River (Collins River basin) at Tenn. St. Hwy. 55 in McMinnville, lat. 35° 40-41' N, long. 85° 46-47' W, 25 August 1967, (5), UT 91.109; Collins River, 5.7 miles SW of McMinnville on Tenn. St. Hwy. 8, lat. 35° 37-38' N, long. 85° 41-42' W, 17 July 1964, (5), TU 33479; Barren Fork River at Tenn. St. Hwy. 55, lat. 35° 40-41' N, long. 85° 46-47' W, 3 May 1972, (1), UT 91.645; Charles Creek (Collins River basin) at Tenn. St. Hwy. 56, lat. 35° 43-44' N, long. 85° 47' W, 4 February 1967, (1), UT 91.48; Charles Creek at Tenn. St. Hwy. 56, 3 October 1971, (39), CU 53474; Hills Dry Creek (Collins River basin) at County Road 4398, SE McMinnville, lat. 35° 34-35' N, long. 85° 40-41' W, 3 October 1971, (11); unnamed spring trib. to West Fork Hickory Creek (Collins River basin) at County Road 4258, 0.4 mi. SE West Fork Hickory Creek, lat. 35° 34-35' N, long. 85° 53' W, 26 November 1972, (1). WARREN-VAN BUREN COUNTY LINE, Rocky River, 15 mi. E McMinnville at Tenn. St. Hwy. 30, lat. 35° 44-45' N, long. 85° 35-36' W, 11 April 1963, (2), TU 30316; Rocky River at Tenn. St. Hwy. 30, 9 July 1969, (18), Rocky River at Tenn. St. Hwy. 30, 3 October 1971, (19). WHITE COUNTY, Calfkiller River at U.S. Hwy. 70, Sparta, lat. 35° 55-56' N, long. 85° 28-29' W, 15 June 1968, (11), AU 3234; Town Creek (Calfkiller River basin) at U.S. Hwy. 70, W Sparta, lat. 35° 56-57' N, long. 85° 29-30' W, 15 June 1968, (3), AU 3218; Wildcat Creek at County Road 4396, NE Sparta, lat. 35° 56-57' N, long. 85° 25-26' W, 8 September 1969, (22), Wildcat Creek at County Road 4396, NE Sparta, 7 October 1972, (81) TU 83150.

The following material was used for comparison with the new species: *Etheostoma atripinne* from a number of localities in Tennessee, *E. duryi* from Alabama and Tennessee, *E. coosae* from Tennessee, *E. simoterum* from several localities in Tennessee.

Diagnosis.—Darter of medium length (see section on *Size*); upper lip usually not bound to snout by frenum; posterior half of breast typically with embedded scales. Dorsal saddles usually 8; numbers 5 and 6 may be fused forming 7 saddles; number 2 may be broken producing 9 saddles. Saddles 1 (completely anterior to insertation of spinous portion of dorsal fin), 4 (caudal end of spinous portion of dorsal fin) and 7 (caudad of soft-rayed portion of dorsal fin) darkest. Males typically with broken bands of dark red pigment above and below lateral line, forming two jagged lateral stripes three scale rows above and one scale row below lateral line, ventral stripe less distinct. Females usually with jagged lateral stripe of dark red pigment on two scale rows above lateral line, usually present on row below lateral line. Alternating broken pale and solid dark horizontal lines along sides; ventrad stripes may be less distinct in some males or lacking in females. Anal fin with basal red band; caudal fin with central red blotch. Gular area and anterior portion of branchiostegal membranes with orange erythrophores. Bases of pelvic fin membranes 2-5 with erythrophores forming red streaks.

Description.—Snout steeply declivous; premaxillary frenum variable, lacking to moderately developed; nape distinctly humped, usually decurving sharply to occiput. Branchiostegal membranes broadly connected, rays 5-5; pectoral fin (237) typically longer than head (223); eye length (58) greater than snout (43). Lateral line complete, slightly arched anteriad; scales moderate in size (45-57 in lateral line); scale rows around caudal peduncle usually 19 (range 17-22); transverse scale rows usually 13 (range 13-15) from anal fin origin, usually 12 (range 11-13) from origin of soft-rayed dorsal fin portion; scale rows above lateral line typically 5 or 6. Vertebrae 38 or 39; dorsal fin usually with XI (range IX-XIII) spines, and 11 (range 10-12) soft rays; anal fin spines II, first largest; anal soft rays typically 7 (range 6-8); branched caudal fin rays usually 15 (range 13-15); pectoral fin rays 14 or 15. Supratemporal canal complete with 6 pores; postorbital,

interorbital, posterior nasal and anterior nasal pores present; single coronal pore; infraorbital canal complete with usually 8 (range 7-10) pores; preoperculomandibular canal pores usually 9 (range 7-9). pores usually 9 (range 7-9).

Breast naked anterior half, squamation variable caudally, embedded, rarely lacking. Cheeks completely scaled in both sexes, exposed on upper half, embedded lower or completely exposed in males; exposed on upper, embedded lower or completely embedded in females. Dorsal saddles 4-9 scale rows in length. Lateral blotches 3-6 scale rows in width. Nuptial tubercles absent. Genital papilla sexually dimorphic, long, subcylindrical tube in breeding females (Fig. 1b); blunt, much shorter and narrower, varying from subconical to subcylindrical in breeding males. Dark subocular and preorbital bars, latter passing beneath anterior nares but not reaching premaxillae. Three small caudal spots, ventral member may be lacking, middle may be coalesced with lateral blotch. Lateral blotches 8 or 9 (range 7-10), rounded, may be discontiguous or connected by narrow band below lateral line. Dorsal saddles usually 8, numbers 5 and 6 may be fused, forming 7 saddles, number 2 may be broken, producing 9 saddles. Saddles 1 (completely anterior to insertion of spinous dorsal fin portion), 4 (caudal end of spinous portion of dorsal fin) and 7 (caudad of soft-rayed portion of dorsal fin) darkest. General body outlines as indicated in Figs. 1a-c. General body proportions indicated in Table 1.

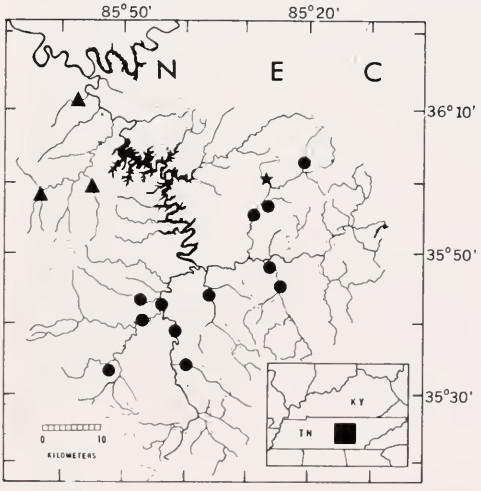

Figure 4. Distribution of collections of *Etheostoma* (*Ulocentra*) *etnieri* (circles) and *E.* (*U.*) *atripinne* (triangles) in the Caney Fork River system, Tennessee. Star symbol indicates type-locality for *Etheostoma etnieri*. N: Nashville Basin. E: Eastern Highland Rim. C: Cumberland Plateau.

Coloration, Holotype, Male.—Breeding males more brilliantly colored and melanistic than females or non-breeding males. Following data taken from holotype, breeding male, immediately after preservation on 18 March 1973. Scattered melanophores on lips with concentration on middle portion of upper lip. Melanophores concentrated on occiput, temporal region, opercles, snout and on eye above pupil. Throat and branchiostegal membranes with distinct, evenly scattered, discrete melanophores. Gular area and anterior portion of branchiostegal membranes with orange coloration. Lower branchiostegal rays and membranes with melanophores concentrated proximally. Head and breast green; pupil green-yellow; iris black. Exposed surface of scales with melanophores concentrated marginally with few, if any, over central portion; however, melanophores in underlying epidermis appearing through central portion of translucent scales. Alternating broken pale and solid dark lines; five pale and six dark horizontal lines above lateral line, four and five below. Lateral line mostly depigmented anteriad. Three vertical spots on caudal peduncle, middle one coalesced with last lateral blotch. Dorsum with 8 quadrate blotches or saddles, numbers 1, 4 and 7 darkest; first saddle located cephalad to first dorsal spine; second located at insertion of spinous dorsal fin portion; third at middle of spinous portion of dorsal fin; fourth at dorsal fin portion; third at middle of spinous portion of dorsal fin; fourth at

termination of spinous dorsal fin portion; fifth just behind insertion of soft-rayed portion of dorsal fin; sixth at middle of soft-rayed dorsal fin portion; seventh immediately caudad to soft-rayed portion of dorsal fin; eighth broken by lightly pigmented area and extending onto procurrent caudal fin rays. Nine rounded lateral blotches, numbers 1 and 4 connecting dorsal saddles 1 and 4 respectively; first blotch located caudoventrad to first dorsal saddle; second beneath insertion of spinous portion of dorsal fin; third under middle of spinous dorsal fin portion; fifth at insertion of soft-rayed portion of dorsal fin; sixth under middle of soft-rayed dorsal fin portion; seventh under termination of soft-rayed portion of dorsal fin; eighth on caudal peduncle caudad to soft-rayed portion of dorsal fin; ninth on caudal peduncle between procurrent caudal fin rays. Sides with dark red pigmented areas forming wide jagged line, 3 scale rows above and two scale rows below lateral line, ventral stripe less distinct. Ventral and ventrolateral areas bright red to brick red in breeding males (fading to orange or orange-yellow in non-breeding specimens). Genital papilla white, immediate surrounding area gray. Spinous portion of dorsal fin with numerous discrete melanophores over spines and interradial membranes; submarginal band occupying last 5 (range 4-6) interradial membranes, consisting of proximal area of melanophores and distal area of erythrophores in last 3 interradial membranes. All interradial membranes with several large concentrations of melanophores of varying intensities. First interradial membrane with red ocellus in lower half adhering to first dorsal spine. Ocellus with black margin on area contiguous with interradial membrane. Coloration of membranes of soft-rayed portion of dorsal fin as follows: (1) basal black band of concentrated melanophores from proximal one-eighth of first interradial membrane, sloping posteriorly to proximal one-sixteenth of fifth interradial membrane; (2) narrow dusky band of scattered melanophores extending from first interradial membrane and forming basal band from sixth interradial membrane to eleventh, band occupying one-eighth of first interradial membrane decreasing in size caudally; (3) second black band of concentrated melanophores extending from first to fourth interradial membranes, occupying one-eighth of first interradial membrane decreasing slightly in width posteriorly; (4) second dusky band occupying first 3 interradial membranes, decreasing from width of one-eighth of first membrane to one-sixteenth of third; (5) red band of erythrophores beginning in second inter-

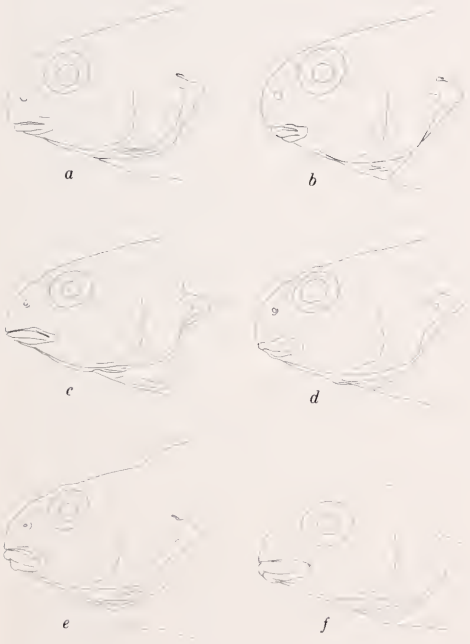

Figure 5. Snout profiles in five species of *Etheostoma* (subgenus *Ulocentra*) a. *Etheostoma simoterum*, adult male, S.L. 46.4 mm (UT 91.333). b. *Etheostoma atripinne*, adult male, S.L. 45.5 mm (UT 91.150). c. *Etheostoma coosae*, adult male, S.L. 52.5 mm (UT 91.147). d. *Etheostoma etnieri*, adult male, S.L. 52.6 mm (USNM 214172). e. *Etheostoma duryi*, adult male, S.L. 46.2 mm (UT 91.628). f. *Etheostoma duryi*, adult male, S.L. 35.6 mm (UT 91.841).

radial membrane widening and increasing in intensity caudally, occupying most of caudal half of fin and most outstanding aspect thereof; (6) submarginal band of concentrated melanophores forming black band from second to eleventh interradial membranes. Remaining portion of fin consisting of mixed erythrophores and melanophores. Procurrent caudal fin rays green; caudal fin with large melanophores on soft rays, interradial membranes mostly with scattered melanophores at proximal one-third and distal one-fourth, latter forming faint dark margin. Caudal fin with erythrophores located in central interradial membranes, brightest at midline, becoming lighter dorsad and ventrad. Membranes outside last branched ray lacking chromatophores. Prepectoral region with evenly scattered discrete to small stellate melanophores. Pectoral fin base with scattered discrete melanophores. Pectoral rays with concentrations of melanophores, inconsistent in membranes and generally few in dorsal members increasing in number ventrad, mostly proximad. Distal portion of ventral six pectoral rays lacking pigment, forming depigmented lower margin of fin. Pelvic fin base with scattered distinct melanophores, rays and interradial membranes covered with melanophores, especially discrete on membranes. First pelvic ray pale with increasing ray pigmentation distally. Distal portion of ventral four pelvic rays lacking pigment, forming depigmented lower margin of fin. Pelvic fin interradial membranes 2-5 with small amounts of red pigmentation on proximal half. Anal fin with numerous discrete melanophores over spines and interradial membranes. First anal spine with light red coloration. Anal fin membranes listed in sequence from anterior margin colored as follows: (1) anterior and distal portions with red erythrophores, membrane covered with melanophores, most concentrated distally; (2) scattered melanophores and faint red pigmentation in middle of membrane extending to distal margin; (3) gray proximal third, red middle third and black distal third; (4-9) membranes with decreasing width of proximal melanophore band, increasing width and brightness of red erythrophore band and increasing width of distal melanophore band.

Coloration, Allotype, Female.—Females much more somber in contrast to brilliantly colored males. Dominant colors brown and black contrasting sharply with white venter. Some red, orange or yellow on fins, sides and venter. Following data taken from allotype immediately after preservation. Dark suborbital bar, slightly wider than holotype, originating in line with middle of eye and extending ventrad below level of lower jaw, widening distally. Preorbital bar more intensely contrasting with lighter snout, originating in line with center of eye extending anteroventrad below anterior naris but not reaching premaxilla. Lips white with fewer melanophores than holotype. Head with melanophore concentrations greatest on occiput, temporal areas, opercles, snout, caudal half of cheek and eye above pupil. Throat immaculate, branchiostegal rays and membranes with several melanophores proximally. Body scales with melanophores mostly marginally. Lateral line mostly depigmented anteriad. Dorsum with 8 quadrate saddles, numbers 1, 4 and 7 darkest. Position of saddles as in holotype except saddle number 8 entire and more intense. Nine rounded lateral blotches in same general position as holotype but lateral blotches 1 and 4 merge less discernibly with dorsal saddles 1 and 4 respectively. Along sides dark red, jagged, lateral stripe, 2 scale rows wide above lateral line, dorsal row of color extending onto base of caudal fin. Most female paratypes possessing one scale row of red pigment below lateral line. Alternating broken white and solid dark horizontal lines along sides, ventral members may be less distinct or lacking in some females. Ventral and ventrolateral areas mostly without pigment, although scattered melanophores and yellow to orange pigment present, including base of caudal fin. Genital papilla white with scattered melanophores in immediate area caudally and on

either side. Some melanophores on body at base of anal fin. Breast with several scattered stellate melanophores. Spiny and soft dorsal fin portions generally with alternating bands of melanophores on spines. Concentrations of melanophores present on membranes in various areas, mostly on bases of membranes in spinous dorsal fin portion. Red ocellus present on first interradial membrane of spiny portion of dorsal fin as on male, except smaller. Last 4 interradial membranes of soft-rayed portion of dorsal fin with erythrophores incompletely bordered by melanophores. Several erythrophores mixed with melanophores in ray preceding above four. Red band in many specimens slightly more extensive, covering up to six interradial membranes with occasional scattered melanophores. Procurrent caudal fin rays with varying concentrations of melanophores. Caudal fin with alternating vertical bands of melanophores lining rays and on rays of proximal bands; membranes generally immaculate with scattered melanophores proximally. In some specimens erythrophores present in caudal membranes, especially medially. Prepectoral region with blotches. Pectoral fin base immaculate; fin colorless, several scattered melanophores lining rays. Anal fin with scattered melanophores on rays, first spine with several melanophores, second immaculate.

Disposition of types.—The holotype (male) and the allotype (female) are deposited at Tulane University (TU 83147 and TU 83148) as are 11 paratopotypes and 89 paratypes. Additional paratypes are deposited in the following museums: 29 paratypes, University of Alabama Ichthyology Collection; 35 paratypes, Auburn University; 39 paratypes, Cornell University; 22 paratypes, University of Florida Museum; 22 paratopotypes and 18 paratypes, University of Michigan Museum of Zoology; 56 paratopotypes, National Museum of Natural History; 28 paratopotypes and 11 paratypes, University of Tennessee Ichthyology Collection. The x-rays are deposited at Tulane University (TU 1491-1494).

Size.—The largest male has a standard length of 63.7 mm, the largest female 54.7 mm. Both specimens were collected from Charles Creek at Tennessee State Highway 56, Warren County, Tennessee, on 3 October 1971.

Range.—This species is known only from the Caney Fork (Cumberland) River system (Fig. 4). It appears to be limited to streams flowing over the Mississippian limestones of the Eastern Highland Rim. Streams flowing over the sandstone, siltstone and shale deposits of the topographically higher Cumberland Plateau lack members of the subgenus *Ulocentra* in the Caney Fork River system. In general, it appears that those acid to neutral waters flowing over the predominantly sandstone and shale deposits of the Cumberland Plateau and Cumberland Mountains provinces have less diversity and biomass in fishes, decapod crustaceans and molluscs than streams flowing over Ordovician to Mississippian limestone deposits of neighboring geomorphic provinces (Bouchard, in press). Streams draining the Ordovician limestones of the topographically lower Nashville Basin contain the nominal *Ulocentra, E. atripinne.*

Fish associates.—The following list of species follows Bailey *et al.* (1970). Collected with *E. etnieri* at one or more localities were the following: *Lampetra aepyptera, Dorosoma cepedianum, Salmo gairdneri, Campostoma anomalum, Clinostomus funduloides, Hybopsis amblops, H. dissimilis, Notropis ardens, N. chrysocephalus, N. galacturus, N. heterolepis, N. leuciodus, N. rubellus, N. spilopterus, N. telescopus, N.* sp. (*cf. spectrunculus*), *Phoxinus erythrogaster, Pimephales notatus, Rhinichthys atratulus, Semotilus atromaculatus, Hypentelium nigricans, Noturus flavus, Fundulus catenatus, Ambloplites rupestris, Lepomis cyanellus, L. gulosus, L. L. macrochirus, Micropterus dolomieui, Etheostoma blennioides, E. flabellare, E. luteovinctum, E. maculatum, E. squamiceps, E.* sp. (*cf. stigmaeum*), *E. virgatum, Percina caprodes, Cottus carolinae.*

Table 1
Measurements of *Etheostoma etnieri* Expressed as Thousandths of Standard Length.

Locality Number of Specimens	Cherry Creek Holotype 1	Cherry Creek Allotype 1	Cherry Creek Paratopotypes 10	Charles Creek Paratypes 10	Rocky River Paratypes 10
Standard length (mm)	60.4	47.8	43.9-60.4 (51.4)	43.6-63.7 (52.5)	44.2-52.0 (48.4)
Body depth at dorsal origin	215	207	196-222 (212)	201-227 (209)	185-206 (195)
Caudal peduncle depth	113	100	96-113 (105)	102-117 (107)	97-104 (101)
Body width	147	*	135-149 (142)	140-159 (147)	123-142 (134)
Caudal peduncle length	288	305	288-323 (305)	289-329 (309)	279-319 (300)
Longest dorsal spine	169	121	113-169 (145)	119-157 (134)	117-151 (132)
Longest dorsal soft ray	152	123	123-172 (148)	130-170 (146)	138-162 (149)
Caudal fin length	187	180	170-194 (184)	168-190 (181)	174-196 (186)
First anal spine	109	88	83-109 (93)	82-106 (97)	96-116 (106)
Longest anal ray	132	134	132-153 (139)	120-144 (130)	130-160 (140)
Longest pectoral ray	245	230	230-259 (241)	216-239 (226)	235-254 (245)
Pelvic fin length	214	224	197-236 (219)	189-222 (210)	222-244 (232)
Width of interpelvic space	81	69	68-81 (74)	71-78 (74)	73-79 (76)
Head length	224	215	215-233 (224)	182-255 (221)	214-232 (222)
Head depth (at occiput)	174	165	157-181 (168)	152-166 (156)	137-152 (146)
Head width	157	153	144-159 (151)	135-152 (145)	131-141 (135)
Snout length	51	44	42-51 (45)	28-55 (42)	40-51 (43)
Orbit length	60	61	56-63 (58)	49-62 (55)	56-60 (57)
Fleshy interorbital width	45	46	45-52 (48)	43-52 (48)	43-52 (49)
Upper jaw length	66	56	52-67 (59)	45-60 (56)	49-58 (54)
Lower jaw to junction of gill membranes	142	128	128-146 (140)	128-147 (140)	133-145 (139)
Pelvic insertion to junction of gill membranes	144	126	114-147 (132)	125-141 (134)	127-140 (135)

*Ovigerous

Table 2
Lateral-line scale counts in four species of *Etheostoma* (subgenus *Ulocentra*); values for holotype in boldface.

Species and River System	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	N	X̄
etnieri																						
Cumberland R.																						
Caney Fork R.																						
Cherry Ck.				1	2	10	6	10	3	3	8	4	1	1	--	1					50	49.6
Charles Ck.					1	--	1	3	1	3	--	--	1								10	49.8
Rocky R.					2	2	1	1	1	2	1										10	48.7
Hills Dry Br.				1	--	--	--	3	--	1											5	48.6
Cane Ck.							1	--	3	--	--	1									5	50.2
Totals				2	5	12	9	17	8	9	9	5	2	1	--	1					80	49.5
atripinne																						
Cumberland R.																						
Caney Fork R.													2	--	--	4	--	--	2	2	10	57.8
Harpeth R.									1	--	--	2	2	4	--	--	--	--	1		10	54.4
Tennessee R.																						
Duck R.													2	1	3	1	1	--	2		10	56.6
Shoal Ck.							1	1	--	--	--	2	1	2	2	--	1				10	53.7
Flint R.						1	1	--	1	3	1	1	2								10	51.1
Totals						1	2	1	2	3	1	5	9	7	5	5	2	--	5	2	50	54.7
simoterum																						
Tennessee R.																						
Hiwassee R.						1	2	2	--	3	--	2									10	50.0
French Broad R.					1	--	1	1	2	2	2	1									10	50.2
Totals					1	1	3	3	2	5	2	3									20	50.1
duryi																						
Tennessee R.																						
Beaverdam Ck.	1	--	2	1	--	--	3	1	2												10	46.8
Duck R.						2	3	--	2	1	1	--	1								10	49.5
Indian Ck.		1	3	1	2	4	3	3	2	1											20	47.1
Totals	1	1	5	2	2	6	9	4	6	2	1	--	1								40	47.6

Table 3
Number of dorsal spines and soft rays in four species of *Etheostoma* (subgenus *Ulocentra*); values for holotype in boldface.

Species and River System	Dorsal Spines 9	10	11	12	N	X	Dorsal Soft Rays 10	11	12	13	N	$\bar{X}$
etnieri												
Cumberland R.												
Caney Fork R.												
Cherry Ck.			**10**		10	11.0		**10**			10	11.0
Charles Ck.	1	3	5	1	10	10.6	1	9			10	10.9
Rocky R.		2	7	1	10	10.9	1	6	3		10	11.2
Totals	1	5	22	2	30	10.8	2	25	3		30	11.0
atripinne												
Cumberland R.												
Caney Fork R.			6	4	10	11.4		8	2		10	11.2
Harpeth R.			4	6	10	11.6	3	7			10	10.7
Tennessee R.												
Duck R.		2	4	4	10	11.2	1	7	2		10	11.1
Shoal Ck.			5	5	10	11.5		7	3		10	11.3
Flint R.			8	2	10	11.2		6	4		10	11.4
Totals		2	27	21	50	11.4	4	35	11		50	11.1
simoterum												
Tennessee R.												
Hiwassee R.		3	7		10	10.7	1	7	2		10	11.1
French Broad R.		2	8		10	10.8	3	5	2		10	10.9
Totals		5	15		20	10.8	4	12	4		20	11.0
duryi												
Tennessee R.												
Beaverdam Ck.		1	5	4	10	11.3		3	6	1	10	11.8
Duck R.		3	5	2	10	10.9		4	5	1	10	11.7
Totals		4	10	6	20	11.1		7	11	2	20	11.8

Table 4
Number of anal and branched caudal rays in four species of *Etheostoma* (subgenus *Ulocentra*); value for holotype in boldface.

Species and River System	Anal Rays 6	7	8	N	X	Branched Caudal Rays 13	14	15	16	17	N	$\bar{X}$
etnieri												
Cumberland R.												
Caney Fork R.												
Cherry Ck.		8	**2**	10	7.2		2	**8**			10	14.8
Charles Ck.	1	9		10	6.9	1	--	9			10	14.8
Rocky R.	1	8	1	10	7.0		1	9			10	14.9
Totals	2	25	3	30	7.0	1	3	26			30	14.8
atripinne												
Cumberland R.												
Caney Fork R.	2	8		10	6.8		1	8	1		10	15.0
Harpeth R.	1	9		10	6.9		3	7			10	14.7
Tennessee R.												
Duck R.	1	9		10	6.9		2	7	1		10	14.9
Shoal Ck.	2	8		10	6.8		3	6	1		10	14.8
Flint R.	1	8	1	10	7.0	1	2	7			10	14.7
Totals	7	42	1	50	6.9	1	11	35	3		50	14.8
simoterum												
Tennessee R.												
Hiwassee R.	1	8	1	10	7.0	2	4	4			10	14.2
French Broad R.	2	7	1	10	6.9	2	6	2			10	14.0
Totals	3	15	2	20	7.0	4	10	6			20	14.1
duryi												
Tennessee R.												
Beaverdam Ck.		9	1	10	7.1	2	4	3	--	1	10	14.4
Duck R.	4	6		10	6.6		5	5			10	14.5
Totals	4	15	1	20	6.9	2	9	8	--	1	20	14.5

Table 5
Number of pectoral rays (left-right) in four species of *Etheostoma* (subgenus *Ulocentra*); value for holotype in boldface

Species and River System	Pectoral Rays								N	$\bar{X}$
	12-13	13-13	13-14	14-13	14-14	14-15	15-14	15-15		
etnieri										
Cumberland R.										
Caney Fork R.										
Cherry Ck.					**6**	--	--	4	10	14.4
Charles Ck.					4	--	1	5	10	14.6
Rocky R.					7	1	1	1	10	14.2
Totals					17	1	2	10	30	14.4
atripinne										
Cumberland R.										
Caney Fork R.					7	3			10	14.2
Harpeth R.		1	--	--	7	1	--	1	10	14.1
Tennessee R.										
Duck R.					5	4	--	1	10	14.3
Shoal Ck					2	2	--	6	10	14.7
Flint R.					7	--	--	3	10	14.3
Totals		1	--	--	28	10	--	11	50	14.3
simoterum										
Tennessee R.										
Hiwassee R.					7	2	--	1	10	14.2
French Broad R.		1	1	--	6	--	--	2	10	14.1
Totals		1	1	--	13	2	--	3	20	14.2
duryi										
Tennessee R.										
Beaverdam Ck.	1	3	2	--	4				10	13.5
Duck R.					7	--	1	2	10	14.3
Totals	1	3	2	--	11	--	1	2	20	13.9

Table 6

Number of vertebrae and number of dorsal saddles anterior to spinous portion of dorsal fin in four species of *Etheostoma* (subgenus *Ulocentra*); values for holotype in boldface.

Species and River System	Vertebrae 37	38	39	40	N	$\bar{X}$	Saddles Anterior to Dorsal Fin 1	%	1-2	%	2	%	N
etnieri													
Cumberland R.													
Caney Fork R.													
Cherry Ck.		**2**	8		10	38.8	**119**	100					119
Charles Ck.		4	6		10	38.6	40	100					40
Rocky R.		6	4		10	38.3	37	100					37
Totals		12	18		30	38.6	196						196
atripinne													
Cumberland R.													
Caney Fork R.							2	5	6	15	32	80	40
Harpeth R.							6	20	3	10	21	70	30
Stones R.*		4	17	3	24	39.0							
Tennessee R.													
Duck R.							2	8	4	16	19	76	25
Shoal Ck.							1	6	7	44	8	50	16
Flint R.							5	42	7	58			12
Totals		4	17	3	24	39.0	16		27		80		123
simoterum													
Tennessee R.													
Hiwassee R.							11	28	23	58	6	15	40
French Broad R.							65	65	24	24	11	11	100
Clinch R.*		5	14	3	22	38.9							
Holston R.*		4	30	5	39	39.0							
Totals		9	44	8	61	39.0	76		47		17		140
duryi													
Tennessee R.													
Beaverdam Ck.							22	100					22
Duck R.							32	100					32
Dry Ck.*	5	6	7		18	38.1							
Totals	5	6	7		18	38.1	54						54

*data from Bailey and Gosline (1955)

Table 7
Diagonal scale counts in four species of *Etheostoma* (subgenus *Ulocentra*); value for holotype in boldface.

Species and River system	Anal Fin to Spinous Portion of Dorsal Fin									N	$\bar{X}$
	11	12	13	14	15	16	17	18	19		
etnieri											
Cumberland R.											
Caney Fork R.											
Cherry Ck.			4	5	**1**					10	13.6
Charles Ck.			8	1	1					10	13.3
Rocky R.			4	5	1					10	13.7
Totals			16	11	3					30	13.5
atripinne											
Cumberland R.											
Caney Fork R.						1	4	4	1	10	17.5
Harpeth R.				4	1	5				10	15.1
Tennessee R.											
Duck R.					2	5	3			10	16.1
Shoal Ck.				2	6	2				10	15.0
Flint R.			1	6	3					10	14.2
Totals			1	12	12	13	7	4		50	15.6
simoterum											
Tennessee R.											
Hiwassee R.		2	1	6	1					10	13.6
French Broad R.				5	2	3				10	14.8
Totals		2	1	11	3	3				20	14.2
duryi											
Tennessee R.											
Beaverdam Ck.	1	4	2	3						10	12.7
Duck R.			4	6						10	13.6
Totals	1	4	6	9						20	13.2

Table 8
Caudal peduncle scale counts in four species of *Etheostoma* (subgenus *Ulocentra*); value for holotype in boldface.

Species and River system	15	16	17	18	19	20	21	22	23	24	N	$\bar{X}$
etnieri												
Cumberland R.												
Caney Fork R.												
Cherry Ck.			**3**	9	12	4	2				30	18.8
Charles Ck.			1	2	7						10	18.6
Rocky R.			1	1	5	2	--	1			10	19.2
Totals			5	12	24	6	2	1			50	18.8
atripinne												
Cumberland R.												
Caney Fork R.							5	--	4	1	10	22.1
Harpeth R.											10	20.4
Tennessee R.					1	5	3	1				
Duck R.						2	4	4			10	21.2
Shoal Ck.					3	6	1				10	19.8
Flint R.				3	4	3					10	19.0
Totals				3	8	16	13	5	4	1	50	20.5
simoterum												
Tennessee R.												
Hiwassee R.			2	3	2	3					10	18.6
French Broad R.			2	3	3	2					10	18.5
Totals			4	6	5	5					20	18.6
duryi												
Tennessee R.												
Beaverdam Ck.	3	1	6								10	16.3
Duck R.	1	2	7								10	16.6
Indian Ck.	3	4	7	2	4						20	17.0
Totals	7	7	20	2	4						40	16.7

Ecology.—*Etheostoma etnieri* has been collected in a wide range of habitats from springs and small creeks to large rivers. The species has a definite preference for smaller to medium sized streams or creeks and is usually collected in riffles and runs of moderate to low turbulence, especially over a gravel substrate. In larger streams and rivers the species is typically found along the margins. At the type-locality the stream consists of alternating pools and riffles. Covering much of the bottom are large limestone slabs, bedrock, gravel, rubble and a shallow covering of silt in the pools. Cherry Creek varies from approximately 5 to 10 m wide. At the type locality most specimens of *E. etnieri* were collected in riffles or runs over a gravel substrate with scattered rocks of moderate size. The dominant riffle inhabitant in Cherry Creek is *E. blennioides* while *Rhinichthys atratulus* and *Notropis telescopus* are the most common fishes in the pools.

Relationships.—Of the nominal members of the subgenus *Ulocentra, E. etnieri* has its closest affinities with *E. duryi*. As is typical with the subgenus *Ulocentra*, most differences between species are exhibited in coloration and pigmentation.

Major similarities between *E. etnieri* and *E. duryi* which indicate close kinship are as follows: the spinous portion of the dorsal fin may possess a red ocellus on the first interradial membrane, a dark mottled pattern and a single marginal or submarginal band in breeding males (confined to the last 4 to 6 interradial membranes in *E. etnieri*); the venter is brightly colored; a basal red band is present on the posterior portion of the anal fin in breeding males (not present in all populations of *E. duryi*); the premaxillary frenum is lacking (occasional specimens of *E. etnieri* have a moderately developed premaxillary frenum); a band of dark red pigment occurs dorsad to the lateral blotches; development of green in breeding males is limited primarily to the head and procurrent caudal fin rays (*E. etnieri* also develops green on the breast).

Etheostoma etnieri differs from *E. duryi* in the following respects: the breast is usually scaled on the posterior half (usually naked in *E. duryi*); a submarginal band is present on the spinous portion of the dorsal fin in breeding males and confined to the last 4 to 6 interradial membranes (complete marginal band on *E. duryi*); the breast is gray in adult nonbreeding males and green in breeding males (orange in breeding males and yellow to orange in nonbreeding males of *E. duryi*); there is a large red blotch on the central portion of the caudal fin in breeding males (no red on caudal fin of *E. duryi*); a jagged band of broken, dark red pigment occurs along the length of the dorsolateral area (limited to the posterior half of the body and less well developed in *E. duryi*); the lateral blotches are little fused (often fused in adult male *E. duryi*, Fig. 3a); the lateral line is more depigmented; orange pigment is present in breeding males on the branchiostegal membranes and gular area; breeding males exhibit red coloration on the pelvic fins; caudal peduncle scale counts are usually 18 or more (typically fewer than 18 in *E. duryi*—see Table 12).

Streams flowing over Ordovician limestones in the lower Caney Fork River system contain a species of snubnosed darter presently referable to *E. atripinne*. The major differences between *E. etnieri* and Cumberland River system *E. atripinne* are in the development of the premaxillary frenum, pigmentation and coloration. The frenum of *E. etnieri* is usually lacking or poorly developed (occasional individuals do have a moderately developed frenum). The pigmentation of *E. etnieri* is different from any population of *E. atripinne* in the Cumberland system. The dorsal saddle or blotch before the spinous portion of the dorsal fin is divided in *E. atripinne* (Fig. 2c) yielding 9 saddles, as opposed to 8 in *E. etnieri* (Fig. 1c). The usually 8 or 9 well separated lateral blotches of *E. atripinne* (Figs. 2a, b) are strikingly dissimilar to those of *E. etnieri* which usually has 8 slightly contiguous blotches (Figs. 1a, b). Differences in coloration of breeding individuals distinguish *E. etnie-*

Table 9
Diagonal scale counts in four species of *Etheostoma* (subgenus *Ulocentra*); value for holotype in boldface.

Species and River system	Scales Above Lateral Line 4	5	6	7	8	N	$\bar{X}$
etnieri							
Cumberland R.							
Caney Fork R.							
Cherry Ck.	1	20	**9**			30	5.3
Charles Ck.		9	1			10	5.1
Rocky R.		8	2			10	5.2
Totals	1	37	12			50	5.2
atripinne							
Cumberland R.							
Caney Fork R.		1	4	3	2	10	6.6
Harpeth R.			9	1		10	6.1
Tennessee R.							
Duck R.		4	5	1		10	5.7
Shoal Ck.		4	6			10	5.6
Flint R.		10				10	5.0
Totals		19	24	5	2	50	5.8
simoterum							
Tennessee R.							
Hiwassee R.	1	9				10	4.9
French Broad R.		6	4			10	5.4
Totals	1	15	4			20	5.2
duryi							
Tennessee R.							
Beaverdam Ck.	9	1				10	4.1
Duck R.	3	7				10	4.7
Indian Ck.	11	9				20	4.5
Totals	23	17				40	4.4

Table 10
Diagonal scale counts in four species of *Etheostoma* (subgenus *Ulocentra*); values for holotype in boldface.

Species and River system	Soft-rayed Portion of Dorsal Fin to Anal Fin 10	11	12	13	14	15	16	N	$\bar{X}$
etnieri									
Cumberland R.									
Caney Fork R.									
Cherry Ck.		1	**5**	4				10	12.3
Charles Ck.			8	2				10	12.2
Rocky R.		1	8	1				10	12.0
Totals		2	21	7				30	12.2
atripinne									
Cumberland R.									
Caney Fork R.					2	7	1	10	14.9
Harpeth R.				7	1	2		10	13.5
Tennessee R.									
Duck R.				2	6	2		10	14.0
Shoal Ck.				5	5			10	13.5
Flint R.			2	6	2			10	13.0
Totals			2	20	16	11	1	50	13.9
simoterum									
Tennessee R.									
Hiwassee R.		4	5	1				10	11.7
French Broad R.			1	6	3			10	13.2
Totals		4	6	7	3			20	12.5
duryi									
Tennessee R.									
Beaverdam Ck.	3	7						10	10.7
Duck R.		7	2	1				10	11.4
Totals	3	14	2	1				20	11.1

Table 11
A comparison of two subgenera of *Etheostoma*

	Ulocentra	*Etheostoma*
Nuptial tubercles on breeding males	None	Often present (see Collette 1965)
Branchiostegal rays	5 (6 in *E. coosae*)	6 (5 in some populations of *E. zonale*)
Lateral line	Usually slightly arched anteriad	Straight anteriad
Snout Profile	Usually steeply declivous	Declivous
Number of dorsal saddles or blotches	Usually 8 or 9	Usually 4-7
Palatine teeth	None	Often present (see Richards 1966)
Melanism on pelvic and anal fins of breeding males	Pelvic and anal fins black	Scattered melanophores on anal and pelvic fins
Red ocellus on spinous portion of dorsal fin	Often present	Absent

Table 12
A comparison of three species of *Etheostoma* (subgenus *Ulocentra*)

	etnieri	*duryi*	*atripinne*
	Caney Fork River system, Tennessee	Tennessee River system, Tennessee, Alabama	Cumberland River system, Tennessee, Kentucky
Breast squamation	Usually scaled posterior half	Breast usually naked	Breast usually naked
Band on spinous portion of dorsal fin, breeding males	Submarginal band confined to posterior 4-6 membranes	Complete marginal band	Complete marginal band
Breast coloration, breeding males	Green	Orange	Orange
Caudal fin coloration	Red blotch	No obvious bright colors	No obvious bright colors
Dorsolateral coloration	Jagged, dark red band along length of entire body	Jagged, dark red band reduced and confined to posterior half of body	Bright red spots
Lateral pattern	Alternating solid dark and broken pale lines	No alternating dark and pale lines	No alternating dark and pale lines
Pigmentation of lateral line	Depigmented anteriad	Moderately depigmented anteriad	Moderately depigmented anteriad
Premaxillary frenum	Usually lacking	Lacking	Moderately to well developed
Number of saddles or blotches anterior to spinous portion of dorsal fin (Table 6)	Always one	Always one	Usually two, slightly to moderately conjoined c separate
Anal fin coloration, breeding males	Red blotch	Red blotch may be present	No obvious bright colors
Development of green breeding color in males	Present on head, breast and procurrent caudal fin rays	Present on head and procurrent caudal fin rays	Usually present on head, body and procurrent caudal fin rays
Coloration of gular area and branchiostegal membranes	Orange and green in breeding males	Green only in breeding males	Green only in breeding males
Coloration of pelvic fin membranes, breeding males	Red	No bright colors	No bright colors
Caudal peduncle scales	Mode 18 or 19	Mode 17	Mode 20 or more

ri from Cumberland River system *E. atripinne* in the following ways. In *E. etnieri* a series of broken pale and solid dark lines are evident above the lateral line. This character can usually be seen even in non-breeding males, but may be less evident in some females. *Etheostoma etnieri* has a broken, jagged, lateral stripe of dark red pigment above the lateral line. The development of this stripe varies in females and non-breeding males. *Etheostoma atripinne* possesses distinct bright red spots mostly above the lateral line. Bright red areas in the soft-rayed portion of the dorsal fin, anal and caudal fins are distinctive in *E. etnieri*, while *E. atripinne* has a bright red margination on the spiny dorsal fin portion as well as red spots on the membranes. Both species possess a red ocellus margined with melanophores on the first membrane of the spinous portion of the dorsal fin. Green coloration usually is limited to the head, breast and procurrent caudal fin rays in *E. etnieri* as opposed to more extensive green coloration in *E. atripinne*. A comparison of *E. etnieri* with Caney Fork River system *E. atripinne* shows the former to exhibit fewer lateral-line scales (45-57) than the latter (54-61) (see Table 2) as well as lower diagonal and caudal peduncle scale counts (see Tables 7-10).

Present taxonomic research with species of the subgenus indicates a cline between *E. simoterum* and *E. atripinne* in, most notably, scale counts and numbers of saddles or blotches anterior to the spinous portion of the dorsal fin (Tables 2, 6-10). Since the purpose of this paper is to expedite the recognition of *E. etnieri*, no attempt will be made to prove or disprove the hypothesis that *atripinne* is conspecific with *simoterum*, and consequently the other Caney Fork River system *Ulocentra* has been referred to as *E. atripinne*. The hypothesis is simply noted here so that subsequent researchers may take it into consideration. Hopefully the description of *E. etnieri* will inspire further study of this poorly known group of handsome darters.

Etymology.—This darter is named in honor of David A. Etnier, University of Tennessee, Knoxville, in recognition of his contributions to our knowledge of ichthylogy and efforts to preserve Tennessee's rich and diverse aquatic fauna. The vernacular name, cherry darter, is in reference to the type-locality and to the striking red color of breeding males.

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NATURAL INFECTION OF THE SNAIL *BIOMPHALARIA OBSTRUCTA* IN LOUISIANA WITH *RIBEIROIA ONDATRAE* AND *ECHINOPARYPHIUM FLEXUM*, WITH NOTES ON THE GENUS *PSILOSTOMUM* [1]

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ABSTRACT

The tropicorbid snail *Biomphalaria obstructa* was found to be naturally infected with the trematode *Ribeiroia ondatrae* (Price, 1931) and with the metacercariae of *Echinoparyphium flexum*, in southeastern Louisiana. The systematic status of *Ribeiroia ondatrae* in the Americas is discussed.

Records of tropicorbid snails, *Biomphalaria obstructa* (Morelet) from the United States are from Florida near Miami, several localities in southeastern Louisiana, and from Texas. This area of the United States where tropicorbid snails are found represents the northernmost zone of distribution of these and other neotropical planorbids. *B. obstructa* and several other related species are referred to as "tropicorbids" because they used to belong to the genus *Tropicorbis*, which has been brought into synonymy with *Biomphalaria* by the International Commission on Zoological Nomenclature.

In a study of the susceptibility of Louisiana tropicorbids to infection with *Schistosoma mansoni*, and their morphology, distribution and ecology (Malek, 1967, 1969), their natural infection with trematodes was also determined based on the examination of a large number of specimens from several localities. A comparison was made of reported trematodes in the same or related species in the neotropics, and in other planorbids in areas of the United States north of the zone of distribution of the tropicorbids.

MATERIALS AND METHODS

Tropicorbid snails were collected from 24 localities, mostly in southeastern Louisiana. The snails were isolated to check on their cercarial shedding. They were kept under observation for at least a month from the time they were collected from the field to allow immature infections, if any, to reach maturity and the shedding of cercariae. Some of the snails which did not shed cercariae were dissected in order to determine the occurrence of larval stages in their tissues. Associate snails in the habitat were also examined for their trematode infections. Life cycle studies were conducted to determine the identity of some of the larval forms. Trematode eggs from the feces of definitive hosts, which had been force-fed with infective

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larval forms, were incubated in water in petri dishes. Water in the dishes was changed every other day. In addition, fecal sediment was also placed on strips of filter paper in test tubes with about an inch of water following the method which had been advocated by Harada and Mori (1955), and which was adapted for the incubation of helminth eggs (Beaver et al., 1964).

RESULTS

The survey revealed the infection of tropicorbid snails in one population at Willswood Pond, Jefferson Parish, southwest of New Orleans with cercariae proved to be those of *Ribeiroia ondatrae* (Price, 1931), when the experimental life cycle was carried out. In four other populations (Clayton Pond; lake at auditorium, Louisiana State University campus in Baton Rouge; at Bonnet Carre Spillway near Norco, St. Charles Parish, and at Willswood Pond) echinostome metacercariae were found in the tissues of the snails. These proved to be the metacercariae of *Echinoparyphium flexum* (Linton, 1892) Dietz, 1910 when fed to a pigeon. A plagiorchid metacercaria was found in two populations at Blind River, Ascension Parish, and at a bayou along Highway 51, St. John Parish, while in three populations an undetermined strigeid cercaria was found (bayou along Highway 51 near Lake Maurepas; Mississippi Delta at Pass a Loutre, Plaquemines Parish; and Bonnet Carre Spillway near Norco).

1. *Ribeiroia ondatrae* (Price, 1931).

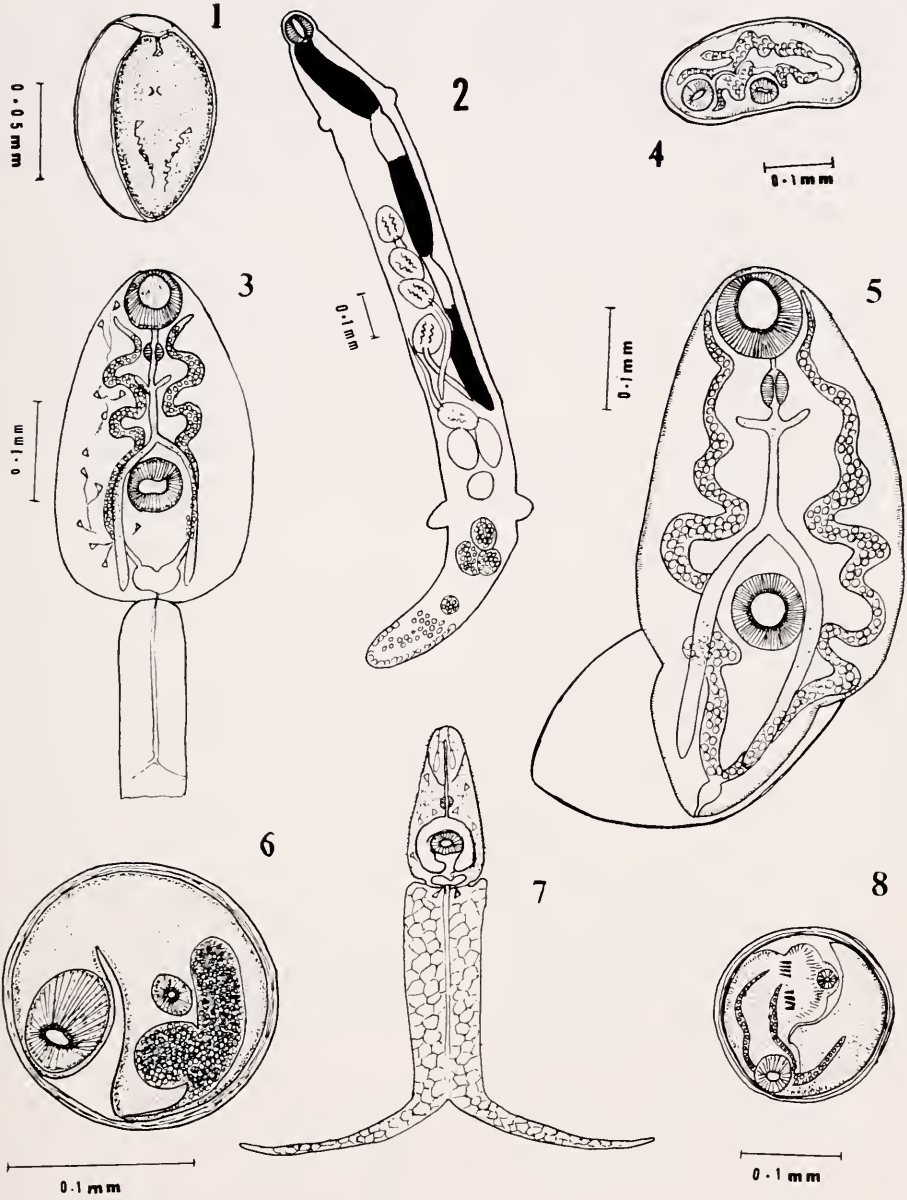
a. *Redia* and *Cercaria*: Daughter rediae (Fig. 2), were recovered from infected snails; mature rediae are orange in color, but young rediae are colorless except for the gut. The gut is about half the length of mature rediae, but more than half the length of immature ones. The redia possesses a "collar" in the anterior region, and two "appendages" in the posterior third of the body. The birth pore is situated immediately behind the collar. An average of 68 daughter rediae were collected from each of snails 7 to 9 mm in greatest diameter.

The cercaria (Fig. 3), emerged from the snails in the early hours of the evening. Morphological details of the cercaria conform with those described by Beaver (1939) for *Psilostomum ondatrae*. Prevalence of infection among *B. obstructa* was four snails out of 62 or 6.5%. Forty-seven *Helisoma trivolvis lentum* from the same habitat were not infected with this fluke.

Apparently cercariae leave the rediae and spend a maturation period in various tissues of the snail, the majority being in the ovotestis and digestive gland region. After leaving the snail the cercariae are active; they swim continuously and they do not tend to concentrate.

b. *Metacercaria*: The cercaria encysted readily in guppies (*Lebisthes reticulatus*) and goldfish (*Carassius auratus*). Fifty cercariae were placed with one guppy, and 18 metacercariae were later recovered from the guppy. The metacercariae (Fig. 4,5) were located in the internal nares and roof of the pharynx; some were found around the eyes; one was found externally at the junction of body and pectoral fin. Inside its kidney-shaped cyst the metacercariae seemed to be highly developed morphologically, and it took a short period in the definitive host for them to develop to adult flukes.

c. *Adult Fluke:* Thirty metacercariae were fed to each of two 3-week old chicks, and 36 cysts were fed to a canary (*Serinus canarius*) but they failed to develop in these hosts. However, when 30 cysts were fed to each of two white mice (*Mus musculus*), eggs were found in the feces eight days later. When the mice were sacrificed two weeks after they were fed the metacercariae an average of 22 adult worms were recovered from the duodenum immediately posterior to the pyloric sphincter. There were large granulomas with areas of hemorrhage and central areas of necrosis. Many eggs were evident in the lesion. The worms were massed within the granulomas in separate pouches or tunnels, and they were very firmly lodged in the tissues with both suckers. The muscularis propria did not seem to be invaded but



Figs. 1-8. Trematode infections of the snail *Biomphalaria obstructa* in Louisiana. 1. Egg of *Ribeiroia ondatrae* from mouse feces, with a fully developed miracidium. 2. Redia of *R. ondatrae* with cercariae, cercarial embryos, germ cells and germ balls. 3. Cercaria of *R. ondatrae* shed by *B. obstructa*. 4. Metacercaria of *R. ondatrae* from a guppy. 5. Excysted metacercaria of *R. ondatrae*. 6. Plagiorchid metacercaria from tissues of *B. obstructa*. 7. Strigeid cercaria shed by *B. obstructa*. 8. Metacercaria of *Echinoparyphium flexum* from tissues of *B. obstructa*.

the mucosa was completely disrupted.

Morphological characteristics of the adult flukes in the present study conform with those described by Beaver (1939).

d. *Egg:* After about 16 days of incubation of eggs in mouse feces fully developed ones were obtained. In each developed egg (Fig. 1), there is a large vacuole pressing and confining the miracidium to one side of the egg. The immature egg measures 84μ by 48μ, while the mature egg measures 98μ by 58μ. Change of the water temperature of the culture stimulated the hatching of the egg, and collection of the miracidia.

2. *Echinoparyphium flexum* (Linton, 1892) Dietz, 1910.

Round echinostome metacercariae (Fig. 8) measuring 0.17 by 0.17 mm were found in four tropicorbid snail populations. The acetabulum measured 0.035 by 0.04 mm. There is a thick cyst wall around the metacercaria, and an outer cyst apparently formed by the host. The metacercariae were found in the kidney of the snail, in the pulmonary wall and in the connective tissue around the rectum. From 22 to 30 cysts were found in each of the infected tropicorbids examined.

The metacercarial cysts were fed to two chicks, and one pigeon. Echinostome eggs measuring 0.08 by 0.05 mm were found in the feces of the pigeon two weeks after the pigeon had been fed. At necropsy adult *Echinoparyphium flexum* were recovered from the pigeon (*Columba livia*).

From one of the habitats where the tropicorbids were collected and found infected with this echinostome (small lake across from auditorium on Louisiana State University campus in Baton Rouge) 31 *Physa anatina* snails were also collected. Two of these physid snails contained metacercarial cysts identical to those found in the tropicorbid snails. Moreover, one physid snail was shedding an echinostome cercaria. When placed in the same container with laboratory-reared tropicorbids and physids the cercariae encysted readily in both species of snails, and metacercarial cysts were recovered from them and were identical to those found naturally in both species of snails.

3. Other trematode infections.

A strigeid cercaria (Fig. 7) emerged from three populations, and is characterized by attenuated long furcae, stout intestinal ceca, penetration glands situated anteriorly at the penetration organ, stout tail and by a spinous cuticle. The cercaria is pharyngeate and with an acetabulum.

Spherical plagiorchid metacercariae (Fig. 6) were found in two populations of the tropicorbid snails. The metacercaria has a thick cyst wall. The excretory bladder is filled with black pigment and excretory products, and has retained its characteristic Y-shape. In some cysts a free stylet was found, apparently after it became detached from the xiphidiocercaria.

DISCUSSION

Beaver (1939) described the life cycle of *P. ondatrae* in Michigan, and agreed with Price's (1931) description and nomenclature. Yamaguti (1958) erected the genus *Pseudopsilostomum* for *P. ondatrae* Price, 1931 (family Psilostomidae), and renamed Beaver's (1939) material *Ribeiroia thomasi* (Family Cathaemasiidae), a scheme followed by Pratt and MacCauley (1961). The reason Yamaguti gave is that he noted that Price (1931) in his description of the type specimen did not mention the esophageal diverticula. Lumsden and Zischke (1963) brought *Pseudopsilostomum* into synonymy with *Ribeiroia* Travassos, 1939, under another family, the Cathaemasiidae. They considered the species *Pseudopsilostomum ondatrae* (Price, 1931) Yamaguti, 1958, and *Ribeiroia thomasi* (McMullen, 1938) Yamaguti, 1958 synonymous with *Ribeiroia ondatrae* (Price, 1931) Price, 1942. Beaver (1939) examined 8 paratypes from USNM Helminth. Coll. No. 29750, and did not overlook the esophageal diverticula in his description and illustrations. Moreover, Basch and Sturrock's description (1969) of a new species, *Ribeiroia marini* (family Cathaemasiidae) from the snail *Biomphalaria glabrata* on St. Lucia is not justified on account of the very little differences in

the number and arrangement of the miracidial plates, and minor differences in the cercaria of *R. marini* and that of *R. ondatrae*.

Basch and Sturrock (1969) considered their cercaria from St. Lucia to be identical with the cercaria from Puerto Rico, also from *Biomphalaria glabrata*. The cercaria was first described from Puerto Rico by Marin (1928) as Cercaria III, and was redescribed by Faust and Hoffman (1934) as a psilostome cercaria, *Cercaria marini*. I believe that *Cercaria thomasi* McMullen, 1938 is synonymous with *Cercaria marini*, and that the same species of fluke *Ribeiroia ondatrae* occurs throughout the Americas. In support of my view that the same species *R. ondatrae* occurs throughout the Americas is that most of the localities where the parasite has been found in the United States and the Caribbean are on bird migratory routes. It is very likely, therefore, that birds carry the infection with the same species from one place to the other, and whichever planorbid snails (*Helisoma* spp. or *Biomphalaria* spp.) are found in the area are utilized as first intermediate host.

Although *Ribeiroia ondatrae* in the present study developed in mice but not in chicks and a canary, birds as hosts cannot be excluded. Beaver's (1939) laboratory experiments with *Psilostomum ondatrae* showed that infection was obtained in chicks, pigeon, duck and canary. Moreover, Price (1931) described the species from the muskrat in Canada, as well as from the California gull from Oregon.

Outside the zone of distribution of *Biomphalaria obstructa* in the United States, infections with *Ribeiroia ondatrae* and *Echinoparyphium flexum* have been reported from other snail hosts. In the midwest Beaver (1939) obtained natural infections with the cercariae of *R. ondatrae* (= *P. ondatrae*) in the planorbid snail *Helisoma antrosum percarinatum* in Michigan, and McCoy (1928) reported that *E. flexum* cercariae encysted in *Physa integra*, and *Helisoma trivolvis* in Missouri. Najarian (1954) found natural infections with *E. flexum* cercariae in *Stagnicola palustris* in Michigan, and showed that the cercariae encysted naturally in *S. palustris*, *Physa gyrina*, and the planorbid *Gyraulus parvus*. Najarian described the life cycle of *E. flexum*, and enumerated later (1961) the differences between the latter species and *E. recurvatum* (von Linstow, 1873) Luhe, 1909. On the bases of the adult morphology, which has a seminal receptacle, the specimens obtained from the pigeon in the present study are *E. flexum*.

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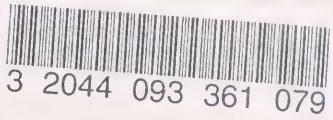
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